

Vol. 20, No. 1

May 1951

THE JOURNAL OF ANIMAL ECOLOGY

EDITED FOR THE
BRITISH ECOLOGICAL SOCIETY

by
CHARLES ELTON
and
DENNIS CHITTY



CAMBRIDGE UNIVERSITY PRESS

LONDON: BENTLEY HOUSE, N.W.1

NEW YORK: 51 MADISON AVENUE

*Annual subscription: thirty-five shillings (twenty-five shillings
to members of the British Ecological Society)*

Single numbers: twenty-two shillings and sixpence

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CONTENTS

	PAGE
F. G. C. Evans. An analysis of the behaviour of <i>Lepidochitona cinereus</i> in response to certain physical features of the environment	1
W. H. R. Lumsden. The night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda. A study in relation to the epidemiology of sylvan yellow fever	11
A. P. Buxton. Further observations of the night-resting habits of monkeys in a small area on the edge of the Semliki Forest, Uganda	31
A. R. Zahar. The ecology and distribution of black-flies (Simuliidae) in south-east Scotland	33
David and Elizabeth Lack. Migration of insects and birds through a Pyrenean pass	63
J. R. Erichsen Jones. An ecological study of the River Towy	68
J. A. Gibson. The 1950 census of gannets (<i>Sula bassana</i>) on Ailsa Craig	87
W. J. McL. Guild. The distribution and population density of earthworms (Lumbricidae) in Scottish pasture fields	88
R. S. Wimpenny. The effect of vegetation on the breeding of newts, <i>Molge cristata</i> and <i>Molge vulgaris</i>	98
Sheila C. Stopford. An ecological survey of the Cheshire foreshore of the Dee estuary	103
T. B. Reynoldson. The dispersal of <i>Urceolaria mitra</i> (Peritricha) epizoic on flatworms	123
N. S. Jones. The bottom fauna off the south of the Isle of Man	132
Reviews	145
Notices of publications on the Animal Ecology of the British Isles	152

AN ANALYSIS OF THE BEHAVIOUR OF *LEPIDOCHITONA CINEREUS* IN RESPONSE TO CERTAIN PHYSICAL FEATURES OF THE ENVIRONMENT

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(With 3 Figures in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	1	6. GRAVITY	6
2. SHORE OBSERVATIONS AND SOURCES OF MATERIAL	2	7. HUMIDITY	7
3. LABORATORY PROCEDURE	2	(a) Rate of water loss in saturated and dry air	7
4. LIGHT	3	(b) Distribution in a humidity gradient	8
(a) Distribution under conditions of uniform light intensity	3	(c) The rate of movement under different conditions of humidity	9
(b) Response to a unilateral light stimulus	3	8. DISCUSSION	9
(c) Aggregation in regions of low light intensity	4	9. ACKNOWLEDGEMENTS	10
(d) Rate of movement in different light intensities	4	10. SUMMARY	10
5. DORSAL CONTACT	6	REFERENCES	10

1. INTRODUCTION

The experimental work included in this paper was undertaken to show the part played by behaviour responses in maintaining an intertidal animal, *Lepidochitona cinereus* (L.) in its characteristic position on the shore. Two questions are involved in the distribution of a shore animal such as *Lepidochitona*: firstly, how the planktonic larvae attain, and settle within, their particular zone on the shore, and secondly, how once established in that zone they maintain themselves there.

Of the first question little is known, for information concerning the settling of chiton larvae, and indeed of most planktonic larvae, is scarce. Colman (1933) has suggested that the larvae of sedentary forms reach their zone as a result of 'hit-or-miss' methods and that only those which settle, by chance, in a suitable zone, survive to reach maturity. Wilson (1937, 1948), however, has shown that in the case of certain polychaete worms metamorphosis may be delayed until a suitable substratum is found, thus increasing the chances of survival. Observations of

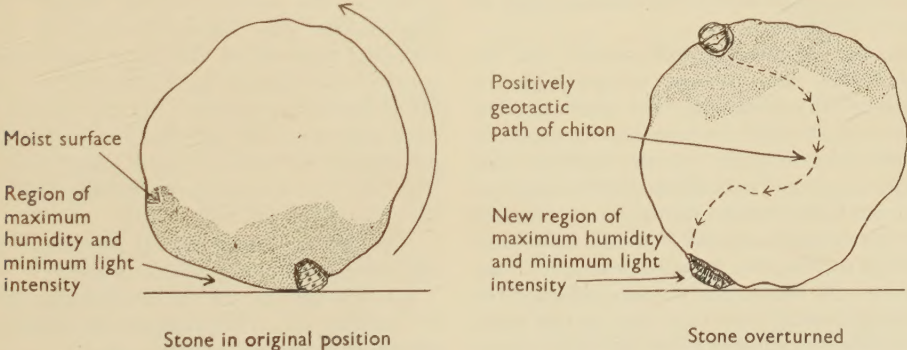


Fig. 1. Diagram of the movements of a chiton when the stone bearing it is overturned—drawn from an observed instance. Approx. $\times \frac{1}{2}$.

like nature have been made on the settling of oyster larvae, which have been found (Cole & Jones, 1949) to settle more readily on shells bearing recently attached spat than on clean shells and shells devoid of spat.

It is with the second question that this paper deals, namely, the way in which the animals once established in their zone, maintain themselves there. This involves an adaptation of behaviour responses to contend with the extreme variability of shore conditions. Many intertidal forms burrow and in this way escape desiccation, others retreat into crevices and pools. *Lepidochitona* when found uncovered by the tide occurs almost invariably on the undersurfaces of stones. If such a stone, bearing beneath it chitons, is overturned on the shore on a bright sunny day, the chitons on top of the stone will be observed to begin moving and, if the surface of the stone is sufficiently moist, to collect again on its now lower surface and so resume their original orientation (Fig. 1).

The chitons in re-orientating themselves in this way resume a position of minimum light intensity, maximum humidity and maximum dorsal contact and, to reach such a position, move with gravity and away from the incident (overhead) light. The experiments which follow are designed to show the extent to which these factors influence the behaviour of the chitons and which are thereby responsible for the situation they occupy within their zone.

2. SHORE OBSERVATIONS AND SOURCES OF MATERIAL

Most of the shore observations recorded in this paper, and on which the experimental work was based, were made at Whitstable where conditions are particularly suitable for a study of this kind. A figure showing the zonation of some of the commoner littoral animals on this shore is given by Newell (1948). The chitons are limited almost entirely to a zone just over 50 yards in width extending from approximately 25 yards below the high-water neap tide level to the seaward edge of the wet part of the *Fucus* zone.

The shore here is covered with pebbles and the chitons were found, almost without exception, on the undersurfaces of the pebbles and were most abundant in the shallow pools which had not been completely drained by the retreating tide. On the landward side the distribution appeared to be limited by the length of time of exposure between tides and on the seaward side by the lack of a suitable substratum. That this factor controlled their distribution at the seaward end of the zone where the soft, sandy mud encroached upon the pebbles was indicated by the facts that on this shore occasional isolated specimens were recorded occurring on stones even down to the low tide level; and that on rocky shores in Cornwall and at Plymouth,

where there was no mud zone, they occurred down to the low-water spring tide level.

Specimens used in the laboratory experiments were usually obtained from Whitstable, but part of the work was done with chitons from Plymouth and Gerrans Bay, Cornwall. Much of this latter material was parasitized heavily with the haplosporidian parasite *Haplosporidium chitonis* Lankester. Heavily infected animals could be detected without dissection, but this was impossible in the case of less heavily parasitized material. In the experimental work both parasitized and unparasitized individuals were used indiscriminately as there were no behaviour differences apparent between them, and even the most heavily parasitized of them appeared to survive as long in the laboratory and to be as responsive as the uninfected specimens.

3. LABORATORY PROCEDURE

In the laboratory the chitons were kept in shallow dishes and transferred from one to another as little as possible. They could be moved about within a dish by a firm, gentle push, but it was found inadvisable to allow the foot to lose contact with the bottom of the dish owing to the difficulties encountered in getting the animals to resettle once they had become detached. In earlier experiments the water was periodically aerated, but this was apparently unnecessary and the animals could be kept for several months in the laboratory in a seemingly healthy condition if the water containing them was shallow and at a low temperature. Nevertheless, throughout the work it was striking how much more uniform and clear-cut were the results obtained from using freshly collected material than were those obtained by using animals which, though apparently normal, had been kept in the laboratory for some length of time.

Observations were made on the reactions of chitons in response to the influence of light, contact, gravity, and humidity stimuli, and experimental details are given in the sections which follow. Preliminary experiments were usually carried out with freshly collected material on the shore and repeated under controlled conditions in the laboratory. Before each set of laboratory experiments the chitons to be used were exposed to daylight and those, if any, which did not exhibit movement within 3 min. were discarded. The rest of the specimens were then placed in darkness for at least 30 min. before use.

The general experimental procedure throughout was arranged where possible to show:

(1) Whether or not the distribution of the animal is a random one if the stimulus is a uniform one and all the other factors are controlled.

(2) Whether or not, when the stimulus is directional, the animal orientates itself to it and moves in a

direction dependent upon the gradient of intensity (i.e. if the response is a 'taxis').

(3) If, when the stimulus is non-directional, it results in a distribution of the animal which can be shown to be dependent upon the effect of the intensity of the stimulus upon the speed or rate of change of direction of the animal (i.e. if the response is a 'kinesis').*

No study has been made of the behaviour of *Lepidochitona cinereus* in direct response to its physiological condition. The effects of hunger, for example, are unlikely to be of great significance biologically to an animal which feeds upon encrusting algae, which are always in abundance in the chiton zone. No evidence has been obtained of a difference in behaviour between the two sexes or at different stages in the reproductive cycle, though it has been recorded by Brewin (1942) that a New Zealand chiton, *Cryptoconchus porosus*, 1 or 2 days before spawning exhibits 'a marked tendency to rise to a position just below the water level and circumnavigate the tank (or rock) until spawning itself commences'.

4. LIGHT

Observations on chitons in their natural environment indicated that they aggregate in positions of low light intensity, and preliminary experiments suggested that the rate of movement of the chitons differs with differing light intensities. This response was investigated as also was the possibility that the animals orientate themselves to a unidirectional light stimulus in a manner similar to that demonstrated by Arey & Crozier (1919) in the Bermudan species *Chiton tuberculatus*.

It was at first hoped to investigate the responses of the chitons to a graded series of light intensities, but in practice only three different sets of conditions were employed: daylight, artificial light and darkness. This was because differences in the response of chitons could only be measured when the differences between the stimuli were great. The intensity of sunlight may be taken to have a value between 500 and 2000 lumens/cm.²/sec., whereas that of the artificial light used was approximately 7 lumens/cm.²/sec.

Most of the experimental work in which artificial light was employed was carried out in a dark-room using a Pointolite lamp. This was calibrated against a standard lamp supplied by Cryselco Ltd. by a null deflexion method using a Megatron photoelectric cell in circuit with a galvanometer. The light intensity employed was approximately 7 lumens/cm.²/sec., though some variation occurred due to mains fluctuations. Additional experiments were made in a

temporary dark-room in Cornwall where a similar light source was used, but the light was of a lower intensity, the current being supplied by a 12 V. car battery.

In order to make observations on the animals' behaviour in darkness a red light was employed. Most records, however, were obtained by examining the mucous tracks which were left by the animals during the experiments. These tracks were made visible by Ulllyott's method (1936*a, b*) of introducing a fine suspension of talc into the dishes at the end of the experiment. The results obtained by these two methods were sufficiently similar to indicate that the animals are completely unresponsive to red light. Ulllyott's method was used to record automatically the tracks of the chitons in experiments in daylight and artificial light.

(a) Distribution under conditions of uniform light intensity

Sheets of glass moistened with sea water and each bearing ten chitons were subjected to overhead illumination. Two were placed in bright daylight, two in artificial light and the remaining two in darkness. After a period of 10 min. the positions of the chitons on the glass sheets were noted and the distance each had travelled was measured. The animals spread in all directions across the glass plate, and the distances travelled depended not only upon the duration of the experiment but also (Table 1) upon the light intensity. In the case of the experiments carried out in darkness, just over two-thirds of the experimental animals showed no movement at all. It may therefore be concluded that the distribution of chitons under conditions of uniform overhead illumination (i.e. a non-directional stimulus) is a random one, but that the rate of movement is greater when the light intensity is great.

Table 1. Distances travelled by chitons under uniform light intensities

Distance moved (cm.)	Daylight	Artificial light	Darkness
0	—	—	14
< 3	1	5	2
3-6	3	11	1
9	7	4	2
12	4	—	1
15	2	—	—
18	2	—	—
21	1	—	—
24	—	—	—
	20	20	20

(b) Response to a unilateral light stimulus

Experiments in which the animals were subjected to unilateral light stimulation were set up in the

* The nomenclature of behaviour mechanisms used here is in accordance with that suggested by Fraenkel & Gunn (1940) modified from Kühn.

dark-room on numerous occasions. In all cases the chitons moved apparently at random, and were never observed to orientate themselves to the incident light. The light intensities employed in these experiments were in the neighbourhood of 7 lumens/cm.²/sec. or about 113,000 ergs/cm.²/sec. Some indication was obtained that chitons orientate themselves to light of the intensity of strong sunlight and move away from it. This suggests a negatively phototactic response; but no experiments were set up to investigate this further owing to the difficulty of introducing a light of sufficient intensity into the dark-room.

The light intensity required to start movement of any kind in *Lepidochitona* under experimental conditions is far greater than that necessary to bring about movement in *Dendrocoelum*. It was shown by Ulliyott (1936a) that *Dendrocoelum lacteum* will react to a beam of light of an intensity as low as 7 ergs/cm.²/sec. Arey & Crozier (1919) showed that in a Bermudan species of chiton, *Chiton tuberculatus*, the response to light was a function of the age of the animal, and that the younger specimens were negatively phototactic whereas the older ones were positively phototactic; but no details were given of the light intensities employed in these experiments. No indications were obtained of any such behaviour differences in age groups of *Lepidochitona*, as indicated by size.

(c) Aggregation in regions of low light intensity

Evidence has already been given that chitons move at random across an experimental dish illuminated from overhead. If, however, a portion of the dish is shaded the chitons tend to collect in the shaded portion. This tendency to aggregate in regions of low light intensity was investigated and a large number of experiments was carried out. The most clear-cut results were obtained when using freshly collected specimens and illuminating them with sunlight. Precautions were taken to prevent any directional factor in the sun's rays affecting the results. The experiments were conducted on bright, cloudy days when the sun was overhead. The experimental dishes, moreover, were arranged in a circle with the centripetal half of each shaded so that the unshaded portions faced in different directions. The results of these experiments are shown in Table 2.

Experiments were also carried out in the dark-room under artificial light. These gave similar results but they were slower to accomplish. This was later shown to be due to the lower light intensities employed. In the case of the dark-room experiments it was necessary to change the water periodically in order to keep down the temperature. Attempts to absorb the heat by passing the light through a trough of water caused so much loss of intensity that little or no movement occurred.

Table 2. *The aggregation of chitons in regions of low light intensity*

(Three different groups (i.e. 30 chitons) observed simultaneously in dishes shaded to cut out directional factors in incident light.)

Duration of experiment (min.)	No. of chitons		No. of chitons		No. of chitons	
	Light	Dark	Light	Dark	Light	Dark
5	9	1	7	3	8	2
10	6	3*	7	3	7	3
15	5	4	7	3	6	4
20	3	6	5	5	5	5
25	3	6	4	6	5	5
30	3	6	3	7	5	5
35	3	6	3	7	5	5
40	3	6	3	7	5	5
45	2	7	3	7	4	6
50	1	8	3	7	4	6
55	1	8	2	8	4	6
1 hr.	1	8	3	7	2	8
2 hr.	1	8	1	9	1	9

* One chiton crawled from the experimental dish.

The experimental results recorded in this section confirmed the view that *Lepidochitona* tends to aggregate in regions of low light intensity. They showed, in addition, that this aggregation takes place more slowly when the light intensity in the unshaded portion of the dish is relatively low. This indicates that the rate of movement of chitons is to some extent dependent on the intensity of the illumination, and measurements of the rate of movement of chitons under different light intensities were made to investigate this relationship.

(d) Rate of movement in different light intensities

In order to investigate the relationship between rate of movement and light intensity, the distances travelled by chitons in (a) sunlight, (b) artificial light, and (c) darkness were measured. The intensity of the artificial light employed was approximately 7 lumens/cm.²/sec., and details of the lamp used and the method of calibration have already been given. Fifteen chitons were placed in Petri dishes filled with sea water and each was exposed in turn to the three different sets of conditions mentioned. After an exposure to a given light intensity a talc impression of the chitons' path was taken and this was then traced on to a sheet of graph paper. The plotted paths were then measured with a Philip's map measurer and the speeds of the chitons calculated. The results are given in Table 3 (compare also Table 1). These and other figures indicated that the rate of movement depends on the illumination and that the greater the light intensity the greater is the rate of movement.

Table 3. *Distances (cm.) moved in 10 min. by chitons under different conditions of illumination*

Sunlight	Artificial light	Darkness
10.6	5.7	0
5.4	3.6	0
8.0	4.6	4.0
8.5	6.3	2.6
6.3	5.0	0
11.0	4.6	0
4.7	4.1	2.0
10.3	7.3	0.9
8.6	6.0	0.5
8.0	4.3	0
4.3	2.0	0
12.3	6.2	4.5
10.6	8.7	2.0
5.4	4.2	1.1
8.6	3.9	3.1
Mean 8.17 ± 0.64	5.10 ± 0.43	1.38 ± 0.41

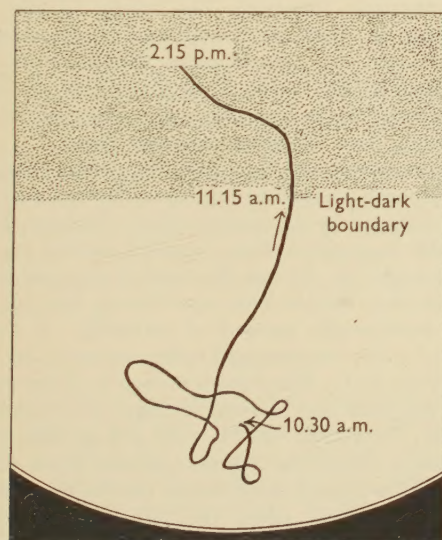
Analysis of variance

Source of variation	Degrees of freedom	Sum of squares	Mean sq.
Within groups	42	160.1074	3.812
Between groups	2	347.1720	173.586
Total	44	507.2794	

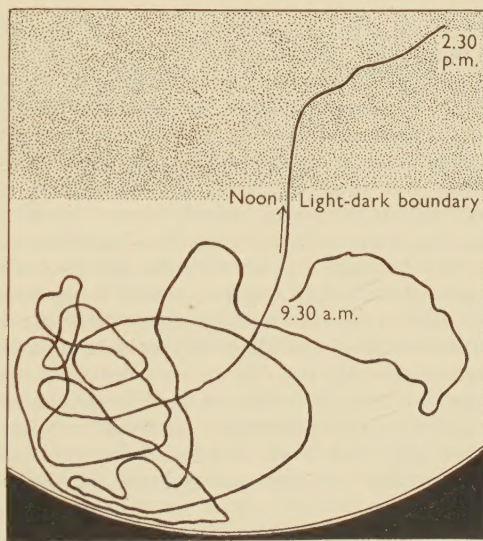
 $F=45.5$. Significant at 1 % level

The duration of each of these experiments was 10 min. This period of time was chosen because on exposure to light there may be a latent period of up to 3 min. in duration before any movement occurs. On the other hand, a longer period of exposure resulted in too great a rise of temperature in those

dishes exposed to artificial light. The use of a light filter was not practical as it cut down the light intensity too severely. It was found that the temperature of the water in the dishes exposed to artificial light rose from 12 to 13.5° C. There was no corresponding rise in temperature in those dishes exposed to sunlight. No allowance has been made for this rise in temperature, but in order to find out whether it affected the interpretation of Table 3 another experiment was carried out to investigate the effect of small differences in water temperature upon the rate of movement of the chitons. Two dishes, each containing ten chitons, were placed in conditions of uniform light intensity. The temperature of the water in one of the dishes was 13.5° C. and that of the water in the other dish was 10.5° C. The chitons were left exposed to these conditions for a period of 10 min. and at the end of this time the tracks were 'printed' and measured and the rates of movement calculated. Approximately every 3 min. the water in both dishes was gently agitated and more water of the requisite temperature was added. As a result the initial temperature difference was maintained throughout the experiment. In a second experiment the dishes were not interfered with and at the end of 10 min. the temperature difference between the water in the two dishes had fallen to just over 2.5° C. The pooled results from these two experiments show that there was slightly more movement in the warmer water, and that the difference only just fails to be statistically significant. Therefore, in the experiment on light intensity (Table 3) the difference in rates of movement observed in artificial light and in sunlight is likely to have been



(a)



(b)

Fig. 2. Movements of two chitons placed in the illuminated halves of Petri dishes. $\times \frac{1}{2}$.

reduced rather than exaggerated by the temperature difference.

The orthokinetic response of chitons to different light intensities results in their tending to aggregate more or less automatically in the shaded regions. The tracks in Fig. 2*a, b* are copies of paths left by chitons placed under water in half-shaded dishes. In both experiments the chitons were placed initially in the illuminated half of the dish exposed to bright, cloudy conditions. Both followed a tortuous path at first: a fairly characteristic initial movement. The path soon straightened out somewhat and, in both instances, led by chance to the shaded area where the movements slowed down and then ceased entirely. In Fig. 2*a* the time spent in darkness was four times that spent in the sunlight; but in that time the animal travelled only one-third of the distance that it travelled when illuminated. In Fig. 2*b* the times spent in light and darkness were equal, but the distance covered in the light was over fourteen times that covered in darkness. It appears, therefore, that negative photo-orthokinesis is an important, if not the most important, factor in causing the aggregation of *Lepidochitona* in dark situations.

Table 4. *Relation between water temperature and rate of movement of chitons in sunlight*

Temp. (° C.) ...	13.5	10.5
No. of chitons ...	20	20
Mean distance (cm.) travelled in 10 min.	8.14 ± 0.86	6.00 ± 0.66

$$t=1.975; \text{ D.F.}=38; P=\text{just} > 0.05.$$

5. DORSAL CONTACT

The fact that, typically, chitons are found beneath stones with their dorsal surfaces in contact with the surrounding pebbles or mud, and that if the stones on which they occur are displaced they tend to resume a position beneath them (see Fig. 1), suggests that they may respond to a dorsal contact stimulus. This possibility was investigated by placing chitons in shallow dishes containing raised sheets of glass supported at their corners by blocks of paraffin wax and arranged at such a height that the chitons could pass under them but in doing so would bring their dorsal surfaces in contact with the glass. Some of the experimental dishes were filled with sea water and the rest were moist, but the chitons in them were not immersed in water. In neither of these sets of experiments did the chitons show any tendency to collect under the glass and it was concluded that no thigmotaxis or allied response was present in *Lepidochitona*.

6. GRAVITY

The influence of gravity was investigated under two sets of conditions: (a) A sheet of glass bearing chitons

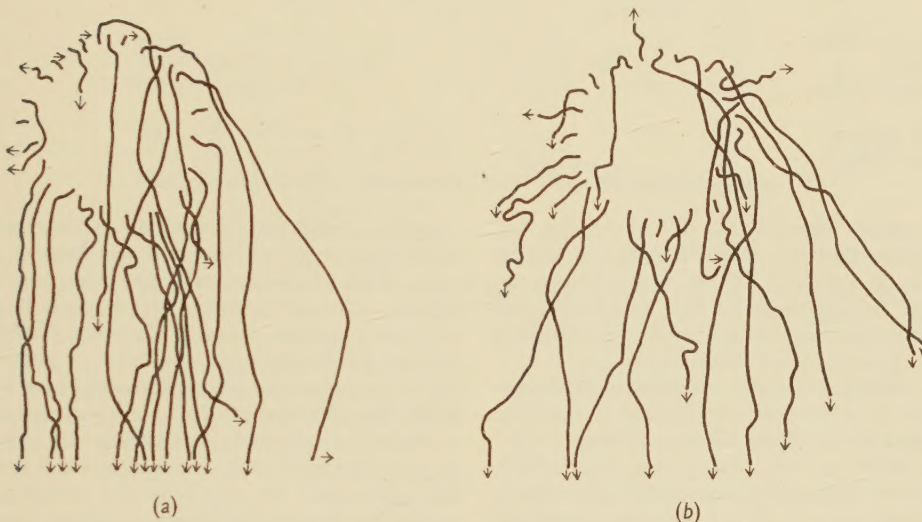
was suspended vertically in a tank of water in conditions of uniform illumination. The chitons moved in all directions across the glass plate and showed no response to the stimulus of gravity. (b) A similar set of experiments was set up, but in which the vertical glass sheet bearing the chitons was not immersed in water. On exposure to the air on a damp surface the majority of chitons showed a marked positively geotactic response and all those which moved any considerable distance tended to move downwards towards the bottom of the glass plate (Table 5*a* and Fig. 3*a*). This is in complete contrast with the previous experiment under identical conditions except that the glass plate was immersed in water. The conclusion is that the responses of the animals vary according to whether they are under water or exposed. Before confirming this view, however, it was necessary to determine whether or not any other factors were involved in bringing about the response. The main alternative possibilities were: (a) that the weight of the chiton's body out of water caused a passive drag downwards across the smooth glass plate; (b) that the water run from the top of the plate to keep the surface moist caused a positively rheotactic response, and it was to this and not to gravity that the chitons were responding.

That the first postulate is unlikely is shown by the fact that the characteristic convex footprints of the chitons are clearly visible in the 'printed' track. This indicates that the route taken is actively controlled and is not the result of passive sliding. A second check on this was made by repeating the experiments with chitons placed on sheets of roughened Perspex instead of smooth glass. The experimental conditions were otherwise identical. The result (Table 5*b*) confirmed the previous finding and all the animals which moved any considerable distance travelled downwards to the bottom of the plate (Fig. 3*b*). Two chitons fell off the Perspex plate when they reached its lower edge; none fell off at any other time.

In order to test whether or not the results obtained on the smooth glass and roughened Perspex surfaces were influenced by the small current which ran down the plates to moisten them, another control experiment was set up. In this the chitons were arranged on a plate as in the previous experiments, but this was placed horizontally instead of vertically. A gentle stream of water was arranged to flow across it, and the plate left for 2½ hr. The chitons moved in all directions across the plate and showed no sign of a rheotactic response. This bears out the view that gravity is the stimulus to which the chitons respond when out of water. It has already been shown that no response to this factor occurs when the animals are totally immersed in water. A similar case of variation of response according to whether an animal is in or out of water has been described by Fraenkel (1927),

Table 5. *Distribution of chitons after 2½ hr. on a damp vertical surface*

		No. of chitons	Orientation of head				No Movement
			Left	Right	Up	Down	
<i>a</i>	Glass plate	26	3	6	—	15	2
<i>b</i>	Perspex plate	26	1	2	1	18	4

Fig. 3. Paths of chitons on vertical plates out of water (*a*) glass, (*b*) roughened Perspex. Arrows show the orientation of the head after 2½ hr. $\times \frac{1}{4}$.

whose analysis of the behaviour of *Littorina neritoides* in relation to natural conditions showed that the response to light was dependent on two factors: whether the animal was in or out of water and whether or not it was upside down. Fraenkel showed it to be always photonegative in response when out of water, but in water to be photopositive when upside down; at other times it was photonegative. Fraenkel, in the course of his paper, correlates this response with the conditions of life of the animal. The success of *Lepidochitona* as a littoral animal may also be to a large extent dependent on the variation of response which it exhibits according to whether it is out of water or immersed in it.

7. HUMIDITY

As inhabitants of the littoral zone, chitons are covered twice daily by the tide. Between tides, however, the stones on which they occur are exposed. The upper surfaces of these stones rapidly dry but their under-surfaces tend to remain damp. It was stated in an earlier section that it is here, in a permanently damp micro-habitat, that the chitons are to be found when the tide is low. Moreover, if a stone bearing chitons

is overturned they move to that part of the stone now underneath, thus resuming a position of maximum humidity (Fig. 1). The following investigations were made to find the sensitivity of chitons to water loss and to test their responses to varying conditions of humidity.

(a) Rate of water loss in saturated and dry air

The chitons used in the following experiments were left undisturbed in an aerated aquarium tank on two weighed glass plates for 24 hr. prior to use. The plates were then removed, wiped, and the chitons on them dried with blotting-paper. The plates bearing the chitons were then weighed and each was suspended in a closed chamber. One was placed in a chamber containing calcium chloride, and in which no moisture could be detected in the air, the other contained a dish of water and the air in it was saturated. Weighings were made at intervals during the experiment. The glass plate from the humid chamber was always carefully blotted before weighing in order to prevent any water which might have condensed upon it from falsifying the results.

Table 6. *The rate of water loss of chitons in wet and dry air*

	Time	Number of chitons		Total weight (g.) of chitons	
		Dry chamber	Wet chamber	Dry chamber	Wet chamber
	Wed. 11 a.m.	14	14	1'407	1'444
	1 p.m.	13*	14	1'148	1'377
	6 p.m.	13	12*	1'146†	1'128
	Thur. 9.30 a.m.	13	12	0'623‡	1'128
	11.30 a.m.	13	12	—	1'128
Av. weight per chiton at beginning	—	—	—	0'100	0'103
Av. weight per chiton at end	—	—	—	0'048	0'094
Percentage loss of weight per chiton	—	—	—	52	8.7

* Chitons dropped off plate. † 2 chitons dead. ‡ All chitons dead.

Table 6 shows that all the chitons in the dry chamber died but that those in the chamber containing saturated air all survived. These results show the sensitivity of chitons to water loss and are in full accordance with the fact that under natural conditions the animals always occur in damp situations.

Yet more striking were the results of experiments carried out to show the rates of desiccation of chitons in moving and dry air. Two batches of chitons were allowed to settle on dry stones and then gently blotted to remove all surplus water. Half of the stones were then removed to a closed chamber containing dry air and the rest were placed in a position exposed to wind and sunshine. The criterion used in assessing the results of the experiment was the length of time taken for the animals to reach a degree of desiccation from which recovery was impossible. Although these conditions could not be accurately controlled it was found that an exposure of 60 min. was sufficient to desiccate the largest chitons used, whilst chitons of 1 cm. in length and less were usually desiccated in under 30 min. These results show that the drying power of the sun and the wind to which the chitons may be exposed when on top of a stone is sufficient to bring about the death of the largest specimen within an hour. Owing to the fact that, at Whitstable, *Lepidochitona* is restricted almost entirely to a zone above half tide level where the average exposure per tide is approximately 9 hr., these animals stand but little chance of surviving these conditions unless they spend this time in a sheltered position beneath the stones where they are protected from the desiccating power of the sun and the wind.

(b) Distribution in a humidity gradient

In order to investigate whether chitons respond to differences in the humidity of the air a humidity chamber was set up. This consisted of a cylindrical glass chamber 18 in. in length and containing at one end a dish of calcium chloride and at the other end a dish of water. A plate of perforated zinc was placed

over these dishes and the entrance to the chamber was at the damp end and consisted of a sheet of vaselined glass. This chamber was placed in conditions of uniform light and temperature, and left overnight in order to establish a steady humidity gradient. Ten chitons, previously kept in a tank in a dark-room for 2 hr., were inserted into the chamber on a sheet of glass. The glass was carefully dried and surplus water removed from the surface of the chitons. It was hoped to see whether or not the distribution of the animals was influenced by the humidity gradient. After 30 min. the animals had scattered about the centre at which they were originally placed, but after this, movement soon ceased. The girdles of the animals were applied firmly to the glass and no further movement occurred. In other experiments using this apparatus similar results occurred. There was movement initially but this was not maintained (Table 7).

Table 7. *Distribution of chitons after 30 min. in a humidity chamber*

(Each division is 3 cm., and animals were introduced into the central one.)

	Drier side		Central	Dampier side	
	1-3	3-6	3 cm. 6-9	9-12	12-15
Exp. 1	.	3	3	4	.
Exp. 2	.	3	5	1	1
Exp. 3	1	5	2	1	3
Total	1	11	10	6	4

The chitons in this experiment were removed directly from an aquarium tank in the dark-room and their introduction into the humidity chamber must have resulted in a considerable increase in the humidity of the air in their immediate vicinity. In an endeavour to prevent this, further experiments were carried out prior to which the chitons were left in the dark-room out of water on a dry glass plate for 30 min. These chitons kept their girdles firmly applied to the glass and did not move even when placed in a chamber

where the air was fully saturated. When placed in a gradient of humidity they either died at the dry end or remained alive and motionless at the damp end. It was therefore concluded that *Lepidochitona* is not sensitive to a humidity gradient. As the chitons traversed smooth glass, ground glass or stone surfaces with apparently equal facility when the surfaces were moist, but did not move across them when dry, it is concluded that dry surfaces provide a mechanical bar to progress.

(c) *The rate of movement under different conditions of humidity*

It has been concluded from the results of the humidity chamber experiments recorded in the last paragraph that on a dry surface, even when the air is saturated, the chitons do not move. However, the following experiments were conducted before those in the humidity chamber and they bring to light the important fact that under very moist conditions the chitons move across a damp surface faster than when actually under water. Chitons were placed, one to each Petri dish, in the dark-room for a period of 60 min. At the end of this time the water was poured from the dishes without disturbing the attached chitons and the bottoms of the dishes were wiped to remove existing mucous tracks. The individual observations in this set of experiments were not made simultaneously but over a period of 2 days. The results are given in Table 8. The general experimental procedure was as follows: one-third of the Petri dishes (Group A) were completely refilled with water, another third were covered with a surface layer of water which did not completely immerse the contained chitons (Group B) and the remainder were dried as completely as possible (Group C). Three dishes from each group were then taken and placed in bright overhead sunlight. They were left for 10 min., and then the chitons were removed and their mucous tracks were 'printed' and their length measured with a Philip's map measurer. The results indicated that the rate of movement was very low indeed, but that under moist conditions it was appreciably higher than when the chitons were under water. Similar results were obtained when the groups of chitons were placed (after an hour in darkness) in artificial light and in darkness.

These results confirm those for the responses of chitons to light, namely, that the rate of movement is highest in a high light intensity. In addition they show that it is also influenced by the degree of exposure of the animals. In complete dryness, even when in bright sunlight, movement soon completely ceases. In all cases the chitons move appreciably faster when in very moist conditions than they do in surroundings that are otherwise identical apart from the fact that they are immersed in water. The speed of the chitons moving in moist surroundings, even in

Table 8. *Distances moved in 10 min. under different conditions of humidity*

Illumination	Distances (cm.) moved by individual chitons in 10 min.		
	Under water, Group A	Damp, Group B	Dry, Group C
Sunlight	8.3	10.2	1.7
	5.8	8.5	2.5
	10.8	19.4	0
Av.	8.3	12.7	1.4
Artificial light	4.0	6.7	0
	4.6	6.5	0
	4.7	6.3	0
Av.	4.4	6.5	0
Darkness	0	4.4	0
	0	0	0
	0	0	0
Av.	0	1.4	0

low light intensities, is relatively high. Table 8 indicates that under the conditions considered the rate of movement decreases thus:

Bright sunlight, moist conditions

↓

Bright sunlight, completely immersed

↓

Artificial light, moist conditions

↓

Artificial light, completely immersed

and that in completely dry conditions movement is almost negligible however intense the illumination. The movement recorded under completely dry conditions in the experiments in this section is probably due in the main to the impossibility of thoroughly drying the animals used in the experiments.

8. DISCUSSION

Lepidochitona cinereus is in almost all respects a typical member of the intertidal fauna, and its behaviour in response to certain simple physical features of its environment is adapted to its life on the shore. Light, gravity and humidity all influence its behaviour. The possibility of a response to a dorsal contact stimulus was also considered but no such response was found. *Lepidochitona* possesses an orthokinetic response to a non-directional light stimulus which results in its aggregation in regions of low light intensity. Some indication was also found that the animal possesses a negatively phototactic response to light of very high intensity. It does not move across a dry surface even when the air above it is completely saturated with water vapour. Although no movement occurs under these conditions, the rate of movement of chitons out of water but on a damp surface was appreciably higher than that of chitons completely immersed in water. Chitons are extremely

sensitive to desiccation and are unable to recover from an exposure of 1 hr. in windy, sunny conditions. This implies that if they remain on top of stones out of the water when the tide is low, they suffer desiccation beyond recovery. The response of *Lepidochitona* to gravity is of particular interest as it varies according to the external conditions. When completely immersed in water no gravity response is shown, but when out of water but on a damp surface there is a well-marked positive geotaxis.

The interaction of these responses results in the aggregation of chitons below stones when the tide is low. As the tide falls the stones of the chiton zone become uncovered and the chitons on them, now out of the water, react to gravity by moving downwards. While the surface of the stone is moist they travel at a maximum rate, especially if the light intensity is high. This leads them to the region beneath the stone and here, responding orthokinetically to the low light intensity, they tend to slow down and aggregate. In this way their behaviour mechanism leads them to a damp microhabitat where they are sheltered while the beach is exposed at low tide. When the chiton zone is again covered by the tide, however, the same conditions no longer hold and the behaviour of the chitons is modified accordingly. As all the surfaces of the stones are immersed in water, rate of movement above and below the stones becomes approximately equal, the difference in light intensity above and below the stones becomes much reduced and the geotactic response, so marked when the chitons are out of water, is lost. Hence the chitons under these conditions, where there is no risk of desiccation, though tending to remain below the stones if the water is shallow and the light intensity high, are not restricted to such situations but are free to move and feed on all the surfaces of the stones.

9. ACKNOWLEDGEMENTS

I wish to thank Dr G. E. Newell for the advice and encouragement he has given during the course of this

work and also for his help in collecting and sending specimens at short notice and at all seasons. My thanks are also due to Dr V. Fretter for help with the literature and for useful criticism.

10. SUMMARY

1. *Lepidochitona cinereus* is found usually attached to the undersurfaces of stones, in the intertidal zone.
2. The density of the population falls off towards the shoreward and the seaward limit of the chiton zone on the shore at Whitstable, and is at a maximum at approximately half-tide level.
3. At any level of the shore where *Lepidochitona* occurs, the density of population is greater under stones occurring in pools than under those that are not immersed. This indicates that the microhabitat of the animals is permanently damp despite the rising and the falling of the tide.
4. The influence of certain simple physical features of the environment in bringing about this orientation is considered.
5. The animals collect in shaded areas.
6. Evidence suggests that the animals are able to orientate themselves to a strong directional light stimulus and move away from it but that their distribution is dependent to a large extent on an orthokinetic response to a directional light stimulus, in which the rate of movement is dependent on the light intensity involved.
7. No evidence was obtained of a response to dorsal contact stimuli.
8. *Lepidochitona* exhibits a positive geotaxis when out of water but there is no geotactic response when the animals are in water.
9. No movement occurs on a completely dry surface. The rate of movement on a damp surface, however, is appreciably greater than that of chitons under water.
10. The way in which, by the interaction of these responses, *Lepidochitona* maintains its characteristic position on the shore, is discussed.

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THE NIGHT-RESTING HABITS OF MONKEYS IN A SMALL AREA ON THE EDGE OF THE SEMLIKI FOREST, UGANDA. A STUDY IN RELATION TO THE EPIDEMIOLOGY OF SYLVAN YELLOW FEVER

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(With 6 Figures in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	11	(d) Seasonal variations in the number of monkeys observed	24
2. PREVIOUS INFORMATION	11	(e) The times of entering and leaving the sleeping trees	26
3. THE STUDY AREA	12	(f) Other observations	29
4. THE SPECIES OF MONKEYS ENCOUNTERED	15	7. DISCUSSION	29
5. NARRATIVE AND METHODS	15	8. ACKNOWLEDGEMENTS	30
6. COMPARISON OF THE NUMBERED TREES	17	9. SUMMARY	30
(a) General	17	REFERENCES	30
(b) The tracing of an individual band	22		
(c) The size of the night-resting bands	23		

1. INTRODUCTION

During recent years much information has been gathered regarding the importance of wild animals in the epidemiology of sylvan yellow fever in Africa. That relating to the area in which the present work has been done is reported by Haddow, Smithburn, Mahaffy & Bugher (1947) and their main findings may be summarized briefly here. Immunity to yellow fever was found to be widespread among the monkeys of the lowland Semliki forest but non-existent in any of the many other animal groups investigated. Although the several species of monkey studied had various day-time habits, some keeping purely to the trees and others spending more or less time on the ground, no significant differences in the immunity rates correlated with these particular differences were detected. It was deduced, therefore, that, if a single main vector insect were concerned, all species must be infected at a time and in a place in which they all adopt a like habit. Such a condition is fulfilled at night, as most species sleep in trees during this period. Entomological investigations in the same locality, devoting particular attention to the vertical distribution and daily rhythm of biting by forest insects

(Haddow, 1945; Haddow, Gillett & Highton, 1947), had shown that the most likely vector fulfilling the required conditions was *Aedes (Stegomyia) africanus* Theobald. The present work was undertaken to confirm, and perhaps extend, the premises of the deduction and was begun in January 1948. The observations of the sleeping habits of monkeys here reported have general bearings on the problem of the exposure of wild monkeys to the attacks of biting insects and are therefore considered significant in a consideration of the epidemiology of the extra-human disease.

2. PREVIOUS INFORMATION

Except in the case of a few species, which have been studied closely in captivity, information on the habits of monkeys of a more than anecdotal character is extremely scanty. Besides his personal observations, referring mainly to baboons, Zuckerman (1932) gives a critical review of the literature, and it is from this author that the general conclusions set out below are derived unless otherwise stated.

The social organization of a band of monkeys or apes is based on a continuous sexual cycle uninterrupted by periods of anoestrus, which seems to be general throughout the group. They are usually gregarious, and a band consists of both sexes and various age groups, the adult males being inter-related in a definite, though mutable, scale of dominance. There seems to be a tendency towards polygyny

* This Institute was financed by means of grants made by The Rockefeller Foundation and by the Secretary of State for the Colonies under the Colonial Development and Welfare Acts, and by contributions from the Governments of Uganda, Kenya, Tanganyika, Northern Rhodesia, Nyasaland and Zanzibar.

which Zuckerman considers the main factor leading to the sometimes marked numerical predominance of females among the adult age group of the band. Solitary males, presumably dispossessed of females and excluded from the band, are commonly reported in many species but solitary females seem to be of very rare occurrence. But dispossessed males may not always be solitary; they may be included in large troops along with the more dominant males and their attendant females. Apart from the few more dominant males, Zuckerman observed no incontrovertible signs of leadership, nor of directing communication by cries. Nor did he satisfy himself that definite sentinels were ever posted; any baboon might give the alarm of approaching danger.

Most species are arboreal but many, e.g. *Cercopithecus aethiops* (L.), are not exclusively so (Shortridge, 1934) and some, for example *Erythrocebus* and *Papio* spp., freely frequent the ground (Elliot, 1913).

Bands of numerical strengths between two or three and, for baboons, a hundred or more are quoted. Bands are thought to occupy definite territories (Lydekker, 1893-6); a given band ranges over an area, sometimes with a fairly regular daily routine, and outside this it does not generally trespass. A migration of a band to a new area is reported (*Papio*). A band may scatter widely for foraging during the day but reunites towards nightfall (*Papio*).

Cercopithecus spp. are recorded as sleeping in trees but as not making nests, it being conjectured that they sleep holding on to branches or to each other (Elliot, 1913), and also sometimes on rocky ledges. Sleeping places recorded for *Papio* spp. include a hollow in a cliff partially protected by a large tree, a cave (Marais, 1939), and small cliff crevices opening on to slopes (Zuckerman, 1932). Sclater (1900) mentions the use of trees where cliffs are lacking. In the cases recorded by Marais the whole band occupied a single shelter and in the cliff hollow the baboons crowded together for sleeping, the females and immature individuals being in the centre and the males on the periphery. In Zuckerman's example the band broke up into small parties distributed among many shelters. In one locality the baboons were reported to pass the night wherever they found themselves at nightfall; in another they spent the nine nights on which they were observed always in a particular locality. If molested at dusk or after dark, bands did not move away for more than a few hundred metres. Chimpanzee bands climb trees for food or for sleeping and make rude nests of twigs, new each night.

Some particular information is recorded by Haddow, Smithburn, Mahaffy & Bugher (1947) for the same area as that in which the present work was carried out:

Cercocebus albigena johnstoni Lydekker occurs mainly in uninhabited swampy, mixed forest in bands

numbering 20-40. It is almost entirely arboreal but may come to the ground when frightened; it may also feed on low vegetation. Its main food is the nuts of *Elaeis guineensis* Jacq. but other fruits and green shoots are also taken.

Cercopithecus mitis stuhlmanni Matschie is an arboreal species especially typical of the hill forest but is stated periodically to descend to the lowland forest, particularly in the wetter weather when fruits are plentiful. Its diet also includes insects.

C. mona denti Thomas is confined to the lowland forest. It is considered to be mainly arboreal. Its bands are of large size. Leaves and shoots composed the stomach contents of the only specimen examined.

C. nictitans mpangae Matschie occurs in large bands mainly along the fringes of the lowland forest. It is mainly arboreal but may be seen on occasion on the ground. Its food largely consists of the fruits of *Elaeis guineensis* and other trees, but it also may raid cultivation. Nightly return to a small area, though not necessarily to the same tree, for sleeping, is recorded for as long a period as 18 months.

Papio doguera tessellatus Elliot occurs as a band, estimated at 60 in number, in the area. It is considered essentially ground-dwelling but may feed and sleep in the trees. Its food consists of fruits of *Elaeis guineensis* and other plants and small arthropods. It also may raid cultivation. The territory of a given band is well defined.

Colobus polykomos uellensis Matschie is typically a monkey of the lowland forest. Its bands number 10-20 individuals but solitary males occur. It is a strictly arboreal species coming to the ground only when alarmed. Leaves are almost exclusively its food, those of *Cynometra alexandri* being considered most usual. This species also is recorded as returning nightly to a small sleeping area.

Pan troglodytes schweinfurthii Giglioli occurs in small bands in the lowland forest, each band appearing to keep to its own territory. Figs appear to be an article of diet. These monkeys construct sleeping nests.

3. THE STUDY AREA

The locality selected for study was the Mongiro forest area in Bwamba, West Uganda. It was known to support a monkey population of unusual variety and abundance, and a considerable body of information, relating both to the monkeys and to the biting insects there, had been accumulated. This has largely been already reported by Haddow, Smithburn, Mahaffy & Bugher (1947), and by Haddow, Gillett & Highton (1947) where a general description of the Mongiro area may be found. It is necessary, however, to add certain other details which are of importance to the present study. The botanical nomenclature used follows that of Eggeling (1940). The identification of

all tree species has been checked by comparison of specimens with the Herbarium of the Forest Department, Entebbe.

The area is shown in Fig. 1 which has been constructed mainly by gridding from two series of air photographs. The form lines were sketched in by eye on air photographs under the stereoscope and give the general form of the area, but their intervals are estimated only. The only altitude in the area known from previous surveys was that of the Mbuga hot springs which was about 730 m. (2400 ft.). Certain other details, such as locations of trees studied and so on, were added by rough methods of measurement and triangulation with the compass.

The Mongiro area is on the extreme eastern edge of the Semliki forest where the floor of the Western Rift Valley gives place to rising slopes. At Mongiro these slopes are particularly steep and form an almost plane surface practically uneroded at least in its lower levels. To the north-east and south-west of Mongiro the foothill slopes are more gradual and erosion into deep ravines is marked. The lack of erosion at Mongiro itself seems to be due to the fact that a smooth rock face closely underlies the surface and is even exposed in many places. The effect is that the edge of the lowland forest is clearly defined at the lower edge of the rock face, and only to the north-east and south-west do larger trees give place more slowly to the *Euphorbia calycina* N.E. Br.-*Albizia* spp. scrub which sparsely covers the rising slopes. The base of the slope is buried in a scree of angular boulders and loose soil. This strip is narrowest below the steep rock face and broadens to the north-east and south-west where the slopes are more gradual. It is well drained and its surface rapidly becomes dry between rainy periods. At its lower edge a much more gradual slope ensues which is composed mainly of slimy mud kept perpetually moist by innumerable small perennial seepages which appear below the lower edge of the scree. This strip gradually becomes more water-logged as one proceeds downwards and gives place to marshy conditions on the level floor of the Western Rift Valley. These four different conditions of soil moisture are correlated clearly with different types of floristic covering. The steep and practically uneroded hill slope is subject to rapid run-off of rain, its soil is scanty and in many places non-existent; it is an area of isolated specimens of *Euphorbia calycina* and *Albizia* spp. The well drained scree has, however, a considerable amount of soil and supports a forest of which the commonest tree is *Cynometra alexandri* C. H. Wright. This species does not grow here to great stature, most specimens hardly exceeding 20 m. in total height. The lower boundary of the species is shown in Fig. 1 and follows fairly closely the lower limit of the dry conditions of the porous scree. Although *C. alexandri* is the commonest tree

throughout this belt there are certain fairly well marked differences in the accompanying trees in different parts of the zone. In the most southerly section (Fig. 1, A, B) *C. alexandri* is most nearly a pure stand though there are considerable numbers of *Celtis soyauxii* Engl. and isolated *Albizia* spp., *Lannea welwitschii* (Hiern.) Engl., *Tapura fischeri* Engl. and *Cola cordifolia* (Cav.) R. Br. Between B and C (Fig. 1) *Cynometra alexandri* is nearly equalled in numbers by trees of several species, including *Cola cordifolia*, *Aningeria altissima* (A. Chev.) Aubr. & Pellégr. and *Antiaris toxicaria* (Rumph. ex Pers.) Lesch. There are also a few *Khaya anthotheca* (Welw.) C. DC. and *Pycnanthus kombo* Warb. These trees are almost all of great size, surpassing greatly the *Cynometra alexandri*, and sometimes exceeding heights of 50 m. They form an irregular canopy above any *C. alexandri* and, from viewpoints on the escarpment above the forest, obscure that tree which here forms rather an understorey layer, together with *Celtis soyauxii*. Along the stream there are a few trees which are characteristic of wetter conditions than are general in this area; these include *Tylostemon ugandensis* Stapf and *Mitragyna stipulosa* (DC.) O. Ktze. Between C and D (Fig. 1) the trees are in general again of smaller size and again *Cynometra alexandri* outnumbers easily the other species. *Celtis soyauxii* is again a common tree but always of small size. The area contains also a moderate number of trees which exceed the *Cynometra alexandri* in stature. They are *Pterygota* n.sp., particularly near the rock face, *Antiaris toxicaria*, *Chlorophora excelsa* (Welw.) Benth. & Hook. f., *Xylopia* sp. near *vallotti* Hutch. and J. M. Dalz., *Combretum molle* R. Br., *Ricodendron africanum* Muell. Arg. and *Ficus* spp. The lower parts of this hill slope are open, with isolated trees and low scrub as well as grassland which is subject to burning in each dry season.

The lower limit of *Cynometra alexandri* (Fig. 1) is approximately the upper limit of *Mitragyna stipulosa* (DC.) O. Ktze. which is the most characteristic tree of the next zone. Other dicotyledonous trees present, but in much smaller numbers, are *Pseudospondias microcarpa* (A. Rich.) Engl., *Macaranga schweinfurthii* Pax and *Ficus* spp. *Elaeis guineensis* Jacq. is extremely common in this zone, and though most of the specimens are of small size, growing under the shade of the almost continuous canopy of *Mitragyna stipulosa*, yet many penetrate and compose a part of that canopy. A few isolated specimens of *Elaeis guineensis* occur in the lower part of the *Cynometra alexandri* belt but they do not invade far. To the north-west the *Mitragyna stipulosa* belt gives place to an area in which *Voacanga obtusa* K. Schum. and *Pandanus chiliocarpus* Stapf are the dominant trees. These form a forest with a low and rather discontinuous canopy on very marshy ground.

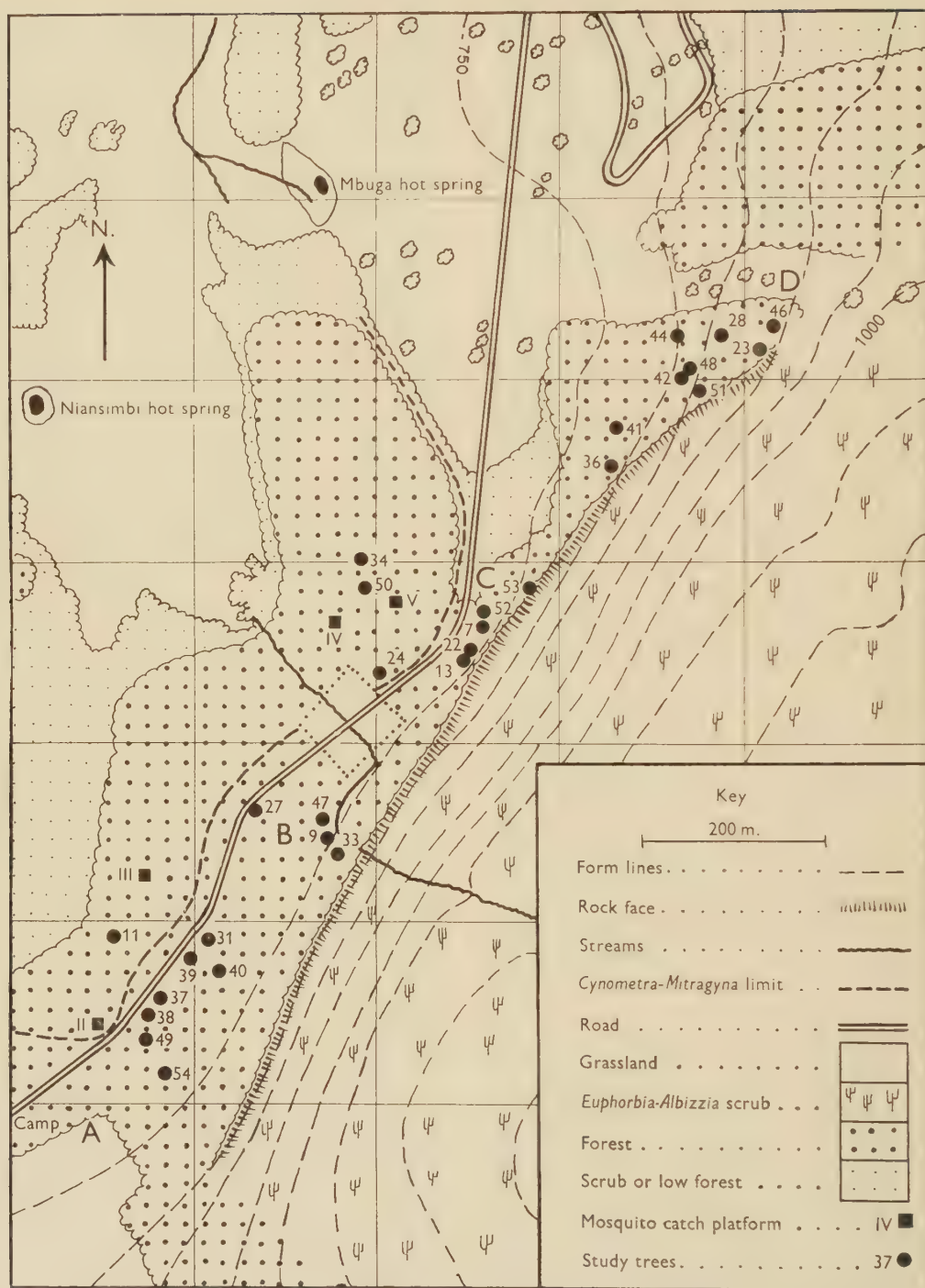


Fig. 1. Sketch map, constructed from air photographs, of the study area at Mongiro, Bwamba, Uganda. Form-line altitudes, in metres, by estimation only.

There are thus two parallel contiguous belts of moderately large or large trees, the *Cynometra alexandri* belt and the *Mitragyna stipulosa* belt. Above and below these belts are areas in which the trees are small and do not form a continuous canopy. Undergrowth in the *Cynometra alexandri* zone is of bushes and small trees of many different species; much of the soil is bare. In the *Mitragyna stipulosa* area the ground is covered by a dense growth of Marantaceae and Zingiberaceae.

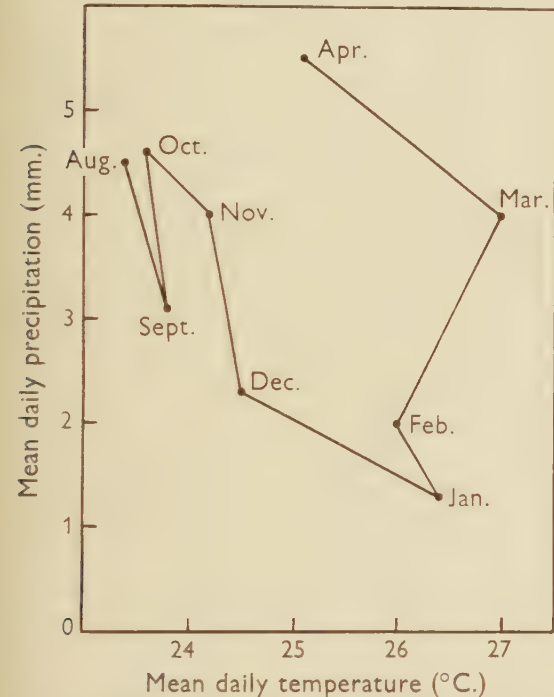


Fig. 2. Climograph of mean daily temperature and precipitation at Hakitengya, Bwamba, by months from August 1948 to April 1949.

Fig. 2 is a rainfall-temperature climograph for Hakitengya, Bwamba, which is considered roughly representative of climatic conditions also at Mongiro. Hakitengya is about 17 km. from and 180 m. higher than Mongiro. Mongiro conditions may be expected to be in general slightly drier and hotter than those at Hakitengya. The climatic conditions in the three observation periods (see p. 16) may be shortly summarized. The first period (10 August to 27 September) was one of cool, rainy conditions. The second (30 October to 22 December) was a period of transition with rising mean temperatures and diminishing rainfall to the third (28 December to 21 February) which covered the driest and hottest part of the year in Bwamba.

4. THE SPECIES OF MONKEYS ENCOUNTERED

The species of Anthroipoidea found in the area, whose habits have been noted in § 2, are set out below. The nomenclature follows that used by Allen (1939) with certain changes as noted.

FAMILY CERCOPITHECIDAE:

<i>Cercocebus albigena johnstoni</i> (Lydekker)	Black mangabey
<i>Cercopithecus mitis stuhlmanni</i> Matschie	Blue monkey
<i>C. mona denti</i> Thomas	Dent's monkey
<i>C. neglectus</i> Schlegel	Brazza's monkey
<i>C. ascanius schmidtii</i> Matschie (= <i>C. nictitans mpangae</i> Matschie of Allen, 1939)	Redtail monkey
<i>Papio doguera tessellatus</i> Elliot	Anubis baboon

FAMILY COLOBIDAE:

<i>Colobus abyssinicus ituricus</i> Matschie (= <i>C. polykomos uellensis</i> Matschie of Allen, 1939)	Lowland colobus
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FAMILY PONGIDAE:

<i>Pan troglodytes schweinfurthii</i> (Giglioli)	Long-haired chimpanzee
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The nomenclatural changes made seem to be well supported by the careful investigation of the matter by Allen (1925), and Dr A. J. Haddow, who has made a thorough study of the matter, confirms this opinion in discussion.

5. NARRATIVE AND METHODS

Elton (1927) has drawn attention to the great value to the ecologist of a consideration of information received from persons who by the nature of their employment or life are perpetually in close contact with animals. Richards (1945) has further pointed out the high utility of natives in floristic work in primary tropical rain forest; many natives are extremely expert in the distinction of tree species by non-floral characters, e.g. the characters of the trunk, bark and slash. At the Field Station in Bwamba there was a nucleus of native assistants, who, from long experience in the hunting of monkeys in connexion with previous epidemiological work in the forest, had had considerable experience in the recognition of the various monkey species present in the area. It was therefore decided to experiment with this personnel, also capable of simple reading and writing, to ascertain if they could be satisfactorily used as observers to locate the main monkey sleeping trees at Mongiro, which was already a locality familiar to them and to the writer. For ease of identification the trees sus-

pected to be used for sleeping were numbered with metal tags nailed to the trunk. During the whole course of the work 51 trees were so numbered, but as three numbers, viz. 6, 43 and 45, were omitted, the highest number actually used was 54.

The first observer arrived in Mongiro on 31 January 1948. He was instructed to visit the area at dusk and dawn and to attach numbers to any trees in which he saw inactive monkeys. He was also required to record, each dusk and dawn, the species, number and activity of monkeys for each numbered tree. Activity was divided into three simple categories for record: (a) inactive monkeys, (b) feeding monkeys, (c) others.

It was expected at this time that the sleeping trees would be few, but by 7 February, twenty-three trees had been numbered and it became obvious that the number of trees used might be large. Nor would it be possible to confirm all the numbered trees as genuine with the few personal visits for which time was available. On the basis of the recorded information ten trees, nos. 1, 3, 5, 8, 14, 15, 16, 17, 18 and 20 were discarded before 11 February. Six of these trees were numbered in error, inactive monkeys never having been reported from them but only moving or feeding monkeys. The remainder were discarded because they were reported untenanted for three or four successive nights. The numbered trees were then divided into two rounds, one in the part of the area south of the clearing and one in the north part, and a separate observer was allotted to each. The number of additional trees which might be added per week was limited. Each tree was regarded as the personal discovery of one or other of the observers and a small money bonus was offered as an incentive to rapid location of the trees used for sleeping, but was not payable until personal visits or extended series of observations made it reasonably likely that the tree was actually in frequent use. This first series of observations terminated on 18 March, when 42 trees had been numbered, and circumstances prevented further work until 10 August 1948.

At the latter time, however, conditions were much more favourable. An experienced and reliable senior African field supervisor was available and was almost constantly allocated to the work. A single observer was allocated to each round of about 14 trees and the supervisor was responsible for checking the observations and ensuring that complete data were returned after each visit. The times of visit were from 05.30 to 07.00 and from 17.00 to 18.30 hr. daily.* Money bonuses were discontinued as being conducive to falsification of data, and a further safeguard was derived from personal unheralded visits to the work

* The 24 hr. clock is used throughout and times are adjusted to the sun, i.e. 06.00 and 18.00 hr. coincide always with sunrise and sunset, respectively.

at irregular intervals. It is on this second series of observations that in consequence practically all the conclusions are based.

The second series may be divided into three successive periods. In the first (10 August to 27 September 1948) observations were made on a total of 28 nights in 4 alternate weeks; in the second and third (30 October to 22 December 1948, and 28 December 1948 to 21 February 1949, respectively) observations were continuous. At the beginning of the first period 7 of the 10 trees which appeared least used on the basis of the previous work were rejected, viz. trees nos. 4, 10, 21, 25, 26, 30 and 32. The highest mean number of bands per 10 nights for any of these trees was 2.86. Of the remaining three least used trees one (no. 42) was retained as it had been observed for only 6 nights, and two (nos. 12 and 19) by error. The latter were rejected early in the first period when 12-14 further nights of observation had failed to discover any inactive monkeys. Three further trees were rejected during this period. Tree no. 2 was destroyed by a storm. Trees nos. 29 and 35 were rejected on the basis of the 21 days' observation, morning occurrences being taken into account; in the later analysis, however, their mean band occurrences per 10 nights (0.95 and 0.96, respectively) exceeded those of five other trees which were retained. Six trees (nos. 46-51) were added during this period.

The criteria for the rejection of trees may have been too rigorous, but except at the beginning when four trees were rejected after only a very short period of observation, the rejected trees were always included among the least used quarter of the total number under observation. Further, none of the rejected trees ever came into use again, though all but one were easily seen from the road. It does appear that the retained trees include the most frequented of the sleeping trees located. However, it was decided at the end of the first period to carry on observations over as long and continuous a period as possible on the trees already under study. Only three trees (nos. 52-54) were added subsequent to this decision.

The small number of sleeping trees located in the *Mitragyna* forest was thought perhaps to be due to the more difficult conditions for observation there. A path was therefore cut in November to allow easy access into another part of it, but no more were located from this path.

It became evident during the work that there were considerable differences among the species regarding the times of settling down for the night and in moving off in the morning. Between 1 and 25 March 1949, timed observations were made in seven of the most frequently used trees. The observers were concealed in viewpoints commanding these trees, and the observation periods mentioned above were divided into 10 min. intervals by a distant drum. Occurrences

in each interval were recorded. A few observations were also made on pet monkeys, secured captive by belt and cord.

The interpretation of records. Certain deficiencies, particularly during the early part of the work, occurred in the observations before the observers became familiar with requirements. Only one deficient observation occurred after adequate supervision could be provided, but it is necessary to remark on the methods of interpretation used. For any given tree, only the nights on which it was visited both at dawn and at dusk were considered. Dusk observations were constantly given priority in importance over those at dawn. Fig. 6 shows that three species of monkey, at least, settle in the trees when the light conditions are still good; at dawn, on the other hand, these species have begun to leave at least 20 min. before sunrise. The continued presence of monkeys up to complete darkness may be confirmed when they have been located previously in a good light. At dawn, on the other hand, it is difficult, before the light strengthens, to pick out monkeys if one lacks precise previous knowledge of their whereabouts.

None of the monkeys recorded shows any obvious modification for nocturnal life such as do the galagos, pottos and the nocturnal monkeys of South America. It is, therefore, reasonable to suppose that, if the presence of monkeys in any given tree is confirmed up to the end of visibility in the evening, they remain there until the morning, though perhaps they may be capable of moving in moonlight. Further, the observers at dusk are usually coming into position before the monkeys and therefore are not liable to deflect them if they remain quiet and concealed. At dawn some disturbance is inevitable in approaching the trees. The monkeys are already in the trees and their absence in the subsequent part of the period may only be due to the fact that they left when the observers were some distance away. Dusk and dawn observations in one night, or observations at dusk only, of inactive monkeys, therefore, both counted as use for that particular night. The species of monkey seen at dusk and dawn of the same night in the same tree never differed, but there were sometimes differences in the numbers counted. Here again the dusk record is given precedence as it is fairly easy to count the monkeys then, while in the morning it is not certain that some have not already left at the time of arrival.

With regard to the reliability of the counts, it is believed that they are very close to actuality. In their actual sleeping positions, three of the four main species at least, viz. *Cercocebus albigena johnstoni*, *Papio doguera tessellatus* and *Colobus abyssinicus ituricus* are not among dense foliage and are fairly conspicuous, the latter particularly so, their black-and-white markings and white tail tuft giving away

their positions immediately. Furthermore, the African observers used are extremely expert at the recognition of animals among foliage and on many occasions their counts of monkeys have been confirmed by the writer, sometimes only after considerable search with prismatic binoculars.

6. COMPARISON OF THE NUMBERED TREES

(a) General

The elimination of trees has been dealt with above and consideration here is limited to a total of 29 trees which were under observation from 10 August 1948, or soon afterwards, until 21 February 1949. These trees (Fig. 1) are set out below and are grouped for convenience in discussion. They are arranged from south to north in each group and closely adjacent trees are joined by brackets.

Group 1. Trees in the *Mitragyna stipulosa* forest:

Tree no.	11	<i>M. stipulosa</i>
	24	<i>M. stipulosa</i>
	50	<i>M. stipulosa</i>
	34	<i>M. stipulosa</i>

Group 2. Trees in the south part of the *Cynometra alexandri* forest:

Tree no.	54	<i>C. alexandri</i>
	49	<i>Cola cordifolia</i>
	{ 38	<i>Celtis soyauxii</i>
	{ 37	<i>Cynometra alexandri</i>
	40	<i>Lannea welwitschii</i>
	39	<i>Chlorophora excelsa</i>
	31	<i>Cynometra alexandri</i>
	27	<i>Aningeria altissima</i>

Group 3. Trees in the *Cynometra alexandri* forest near the Mongiro river:

Tree no.	{ 33	<i>Cola cordifolia</i>
	{ 9	<i>Tylostemon ugandensis</i>
	{ 47	<i>Pycnanthus kombo</i>

Group 4. A group of large trees at the edge of the *Cynometra alexandri* forest:

Tree no.	{ 13	<i>Antiaris toxicaria</i>
	{ 22	<i>A. toxicaria</i>
	{ 7	<i>Aningeria altissima</i>
	{ 52	<i>A. altissima</i>

Group 5. Trees in the north part of the *Cynometra alexandri* forest:

Tree no.	53	<i>Chlorophora excelsa</i>
	36	<i>Pterygota</i> n.sp.
	41	<i>Pterygota</i> n.sp.
	51	<i>Xylopia</i> sp. near <i>vallotti</i>
	{ 42	<i>Pterygota</i> n.sp.
	{ 48	<i>Pterygota</i> n.sp.
	23	<i>Chlorophora excelsa</i>
	44	<i>Riciodendron africanum</i>
	28	<i>Xylopia</i> sp. near <i>vallotti</i>
	46	<i>Combretum</i> ?molle

Table 1. *The use of 29 trees at Mongiro, Bwamba, for sleeping by seven species of monkey from 10 August 1948 to 21 February 1949. Values given are the mean numbers of bands observed per ten nights*

Tree group	Tree number	Number of nights observed	Species							All species
			<i>C. a. johnstoni</i>	<i>C. m. stuhlmanni</i>	<i>C. m. denti</i>	<i>C. neglectus</i>	<i>C. a. schmidtii</i>	<i>P. d. tessellatus</i>	<i>C. a. ituricus</i>	
1	11	137	0.44	0.07	0.07	0.07	1.31	0.22	—	2.18
	24	137	1.02	—	—	—	—	0.15	0.15	1.32
	50	122	0.90	—	—	—	—	2.87	—	3.77
	34	137	1.82	—	—	0.15	0.07	3.06	0.15	5.25
	Total		4.18	0.07	0.07	0.22	1.38	6.30	0.30	12.52
2	54	86	0.35	0.12	—	—	1.05	0.81	0.12	2.45
	49	126	0.63	0.08	—	—	0.63	0.16	—	1.50
	38	137	0.07	—	—	—	0.44	—	—	0.51
	37	137	0.07	—	—	—	0.66	—	—	0.73
	40	137	0.29	—	—	—	0.15	0.07	0.15	0.66
	39	137	0.15	—	—	—	0.07	—	0.29	0.51
	31	137	0.44	—	—	—	0.44	—	—	0.88
	27	137	—	—	—	—	—	—	0.15	0.15
	Total		2.00	0.20	—	—	3.44	1.04	0.71	7.39
3	33	137	1.90	0.22	—	—	0.15	0.22	—	2.49
	9	137	0.58	0.07	—	—	0.07	—	0.07	0.79
	47	128	1.88	—	0.08	—	0.31	0.16	—	2.43
	Total		4.36	0.29	0.08	—	0.53	0.38	0.07	5.71
4	13	137	0.66	0.07	—	—	0.15	1.46	0.58	2.92
	22	137	0.80	0.07	—	0.07	0.51	1.68	0.51	3.64
	7	137	0.73	—	—	—	0.07	0.95	0.22	1.97
	52	88	0.11	—	—	—	—	0.57	0.11	0.79
	Total		2.30	0.14	—	0.07	0.73	4.66	1.42	9.32
5	53	86	0.12	—	—	—	—	0.58	1.40	2.10
	36	137	0.44	0.22	—	—	—	0.15	1.97	2.78
	41	137	0.36	—	—	—	0.07	0.29	1.75	2.47
	51	121	—	—	—	—	—	0.08	1.07	1.15
	42	137	—	—	—	—	0.07	0.29	2.99	3.35
	48	126	0.16	—	—	—	—	0.08	1.35	1.59
	23	137	0.15	—	—	—	0.07	0.07	1.24	1.53
	44	137	0.22	—	—	—	—	—	1.82	2.04
	28	137	0.15	—	—	—	—	0.07	0.51	0.73
	46	129	—	—	—	—	—	—	1.24	1.24
	Total		1.60	0.22	—	—	0.21	1.61	15.34	18.98

Table 1 summarizes the results for the whole series. Values are given for each of the seven species in each tree and are the mean number of bands (irrespective of their numerical strength and including single monkeys) occurring in a standard of 10 nights. Totals of rows (individual trees) indicate the total frequency of use by all species together and allow comparison of different trees. Similar tables were made for each of the three subsidiary periods, but these have been omitted to economize space, and their essential results presented otherwise. Table 2, which is derived from these tables and from Table 1, allots ordinal numbers to each tree in respect of its use by the four common species and for all species for each of the three periods and for the whole series.

It was considered, for comparisons of the frequency

of occurrence of the species within the various tree groups, that it might be advantageous to adjust each group to a standard number of trees; but it is believed that the number of sleeping trees located in any area was probably roughly proportional to the number existing and therefore that a more realistic interpretation may be obtained from simple comparison of the column totals (individual species) through the five groups. The column totals for each tree group for the whole series are derived from Table 1; Table 3 gives these values for four main species in the three subsidiary periods, derived from the tables which have been omitted (see p. 18). Fig. 3 presents these graphically.

Cercocetus albigena johnstoni. Fig. 3 shows that sleeping bands of this species occurred most com-

Table 2. *The order of frequency of use of 29 trees at Mongiro, Bwamba, by the four main monkey species and by all species*

The first, second and third figures horizontally across each species column are ordinal numbers referring to periods 10 August to 27 September 1948, 30 October to 22 December 1948, and 28 December 1948 to 21 February 1949, respectively. The last number refers similarly to the whole series. Blanks indicate no occurrence, and dashes no observation, for period concerned.

Tree group	Tree no.	Species																			
		<i>C. a. johnstoni</i>				<i>C. a. schmidtii</i>				<i>P. d. tessellatus</i>				<i>C. a. ituricus</i>				All			
1	11	11	10	10	11	1	3	1	1	6	12	11					9	12	10	11	
	24	7	2	7	4					9	10	15	14	15		15	19	11	21	18	
	50		3	7	5					1	3	1	2				1	7	1	2	
	34	5	1	2	3		6		12	2	1	2	1	15	10	15	3	1	2	1	
2	54	—	5		15	—	2	1	2	—	7	5	6	—		10	19	—	9	6	9
	49	4		5	9	4	4	4	4	6	10		13					22	22	13	17
	38		14		24	5	4	6	6									25	22	25	27
	37			17	24	3	6	3	3									23	26	18	24
	40		14	10	16	5	6		9		12	19	14		10	15	22	25	20	26	
	39		10		19		6	9	12				9	10	13	21	22	27	27	26	
	31			5	11	5		4	6								25		16	21	
	27												13		15	23				29	
3	33	1	3	3	1		6	9	9	9	10	12	11				6	10	15	7	
	9	2		10	10	5			12				14			21	11	26	25	22	
	47	10	6	1	2	2	6		8	8	10		13				10	13	4	10	
4	13	3	10	10	8			8	9	4	4	3	4	5	9	10	5	8	6	5	
	22		8	3	6		1	6	5	3	2	4	3	9	8	11	8	2	3	3	
	7	7	6	10	7		6		12	4	5	6	5		9	14	18	5	17	14	
	52	—		17	23	—				—	9	7	8	—	14	20	—	21	21	22	
5	53	—	13		22	—				—	7	7	7	—	13	3	5	—	17	9	12
	36	11	9	15	11							11	15	5	1	5	2	13	3	10	6
	41		14	9	14	5			12		10	9	9	7	1	7	4	16	4	13	8
	51											12	17	2	7	8	9	7	18	23	20
	42					5			12		10	9	9	1	3	2	1	2	5	5	4
	48	9		17	18					6			17	3	4	8	6	4	13	23	15
	23			15	19	5			12		10		19	7	11	4	7	16	19	12	16
	44	5			17									9	5	1	3	14	15	8	13
	28		14	17	19					9		10		9	11	10	11	19	19	27	24
	46													4	6	6	7	15	16	19	19

Table 3. *The comparative use of five tree groups by the four main monkey species in the three observation periods*

Data from tables of the same type as Table 1 (column totals in each tree group). The three figures given for each species in each tree group refer to the first, second and third periods respectively.

Tree group	Species			
	<i>C. a. johnstoni</i>	<i>C. a. schmidtii</i>	<i>P. d. tessellatus</i>	<i>C. a. ituricus</i>
1	2.14, 5.06, 4.11	2.50, 0.76, 1.43	10.02, 5.10, 6.25	0.36, 0.38, 0.18
2	1.18, 1.76, 2.86	2.38, 2.00, 5.00	0.59, 0.52, 1.25	2.14, 0.0, 0.54
3	6.60, 2.07, 5.18	1.94, 0.38, 0.18	0.89, 0.38, 0.18	0.36, 0.0, 0.0
4	2.14, 1.89, 2.69	0.0, 0.94, 0.90	4.64, 4.08, 4.81	2.86, 2.20, 0.0
5	2.02, 1.27, 1.79	1.08, 0.0, 0.0	0.95, 0.90, 2.33	21.49, 14.46, 13.40

communicating in many directions with the crowns of other trees of the same species and of *Elaeis guineensis*. Tree no. 24, that of the fourth importance, was closely similar to the latter, except that it was adjoined by a *Pseudospondias microcarpa* and surrounded by less tall *Elaeis guineensis*; it was unbranched to a height of 12 m.

Cercopithecus mitis stuhlmanni. The small number of observations of bands of this species does not allow the definition of any marked preference. It occurred in all five tree groups. The two trees in which it was most frequently observed were nos. 33 and 36. Tree no. 33 was the most preferred tree also by *Cercocebus albigena johnstoni* and has already been briefly described. Tree no. 36 was a *Pterygota* n.sp., a tree of similar type, unbranched to 18 m. and about 30 m. tall with a compact crown communicating with a smaller *Cola cordifolia* and another unidentified tree. It also was close to the rock face.

Cercopithecus mona denti. The two observed occurrences of this species were in trees no. 11 and 47, *Mitragyna stipulosa* and *Pycnanthus kombo* respectively, in tree groups 1 and 3.

Cercopithecus neglectus. This species was observed only four times, in trees nos. 11 and 34 (tree group 1) and in tree no. 22 (tree group 4).

Cercopithecus ascanius schmidtii. In the first period *C. a. schmidtii* was observed in tree groups 1, 2, 3 and 5 and in that order of frequency though the differences are not large. None was seen subsequently in group 5, and group 2 predominated over the others, especially in the third period. Tree no. 11 was the most favoured tree and was consistently so, never falling below third ordinal place in any period. It was a *Mitragyna stipulosa*, unbranched for 12 m. and about 20 m. tall, surrounded closely by other trees of this species and by *Elaeis guineensis*. The tree of second importance was no. 54 and it occupied first or second place in subsidiary periods. It was a large *Cynometra alexandri*, about 25 m. tall with a trunk unbranched until about 18 m. above ground level. Its crown communicated with the foliage of many surrounding trees, mainly *C. alexandri* and *Celtis soyauxii*. Tree no. 37 was the third most popular and was fairly consistently so, though it fell to sixth place in the second period. It was also a *Cynometra alexandri*, about 20 m. tall, forking near its base and with foliage closely approaching the ground. Its foliage communicated with that of four surrounding trees, *Celtis soyauxii*, *Cola cordifolia* and *Albizzia* sp. Fourth tree was no. 49 which was a small *Cola cordifolia* hardly exceeding 15 m. stature and with a small round crown which abutted on those of two small trees, a *Celtis soyauxii* and a *Tapura fischeri*.

Papio doguera tessellatus. In all three periods tree groups 1 and 4 included nearly all the sleeping bands of this species reported, though they were not com-

pletely absent from any of the tree groups. Tree group 1 constantly predominated over group 4 and included the two trees most preferred by this species. Both these trees were consistently occupied; tree no. 34 was never lower than second place and tree no. 50 never lower than third. Tree no. 34 was also much frequented by *Cercocebus albigena johnstoni* and has been briefly described under that species. Tree no. 50 was very similar, being also a *Mitragyna stipulosa* about 25 m. tall, unbranched for 20 m. and closely surrounded on all sides by a mixed canopy of *M. stipulosa* and *Elaeis guineensis*. The trees of third to fifth importance were all in tree group 4. The third and fourth trees were, respectively, nos. 22 and 13, and both were consistently occupied, never falling lower than fourth place. Tree no. 22 was a large *Antiaris toxicaria*, of about 35 m. height, with a huge spreading crown. The trunk was clear for about 25 m. to the first branch but the crown communicated with tree no. 13 and two *Cynometra alexandri*. Tree no. 13 was also an *Antiaris toxicaria* of similar height but with a more compact crown, which was joined by the crest of a much smaller *Celtis soyauxii* and a *Cynometra alexandri*. Its first branch was at about 15 m. height. It is to be noted that the trees described above, with tree no. 7 fifth in order of preference, are all within a small area about 160 m. in diameter. Together, these five trees accounted for 72% of all *Papio doguera tessellatus* bands observed.

Colobus abyssinicus ituricus. During one or other of all three periods, *C. a. ituricus* slept in all five tree groups, but tree group 5 was always overwhelmingly preponderant in importance; it included the first nine trees in order of importance. Tree no. 42, which occupied first place, was regularly used, never falling below third place. It was a *Pterygota* n.sp. about 30 m. tall with a trunk clear to about 15 m. and a large sparsely leaved crown. The crown was joined by another *Pterygota* n.sp. (tree no. 48), by a large *Cynometra alexandri*, and by a *Celtis soyauxii*. There was a large open space on one side of the tree. The tree of second importance was no. 36; it has already been described under *Cercopithecus mitis stuhlmanni*. Tree no. 44 occupied third place; it was only ninth in the first period but rose in importance through the series, occupying first place in the last period. It was a huge *Ricinodendron africanum* unbranched for 15 m. and about 40 m. tall with a broad flattish crown; the foliage of several *Cynometra alexandri* joined the crown. Tree no. 41, that in the fourth place over the whole series, was also irregularly occupied; it varied between first and seventh place in the three periods. It was a *Pterygota* n.sp. about 35 m. tall with a narrow but deep crown whose foliage reached as low as only 10 m. from the ground. The crown was joined by the foliage of several small trees including *Cynometra alexandri* and *Celtis soyauxii*.

The four trees most frequented by each of the four main species may be considered in an attempt to define the attributes of the most popular sleeping trees. As far as baboons are concerned the general location of their main sleeping trees is as might be expected; the band frequented mainly the northern half of the area, favouring particularly the forest fringe and the open ground closely adjacent to it. In the case of their two most frequented trees (nos. 34 and 50), which were both *Mitragyna stipulosa* in the swamp forest, little indication was evident on the matter of preference of some trees over others; *M. stipulosa* is overwhelmingly the commonest tree in the swamp forest and all specimens are remarkably uniform in size and formation. The same consideration applies to the *M. stipulosa* frequented by *Cercocebus albigena johnstoni* and *Cercopithecus ascanius schmidtii*. Yet tree no. 34 was also highly frequented by *Cercocebus albigena johnstoni* so that it appears that it possessed characteristics which rendered it a popular sleeping tree for more than one species. In the hillside forest, however, some of the characteristics of the preferred trees may be distinguished. *Cynometra alexandri*, though it was the commonest tree in the area, was avoided by all four species with the exception of *Cercopithecus ascanius schmidtii*. *Cynometra alexandri* is here a tree generally of small stature, which forks near the ground and is therefore easily climbed. Excluding the trees preferred by *Cercopithecus ascanius schmidtii* all were over 30 m. tall and included only five species—*Cola cordifolia*, *Pycnanthus kombo*, *Antiaris toxicaria*, *Pterygota* n.sp. and *Ricinodendron africanum*. They considerably overtopped the general forest canopy in this area. They were trees with clean trunks in the lower part, none branching laterally below a height of about 15 m. They were free from lianas. *Pterygota* n.sp. seems to be a species of tree preferred by *Colobus abyssinicus ituricus* and *Antiaris toxicaria* by *Papio doguera tessellatus* but these are probably simply reflexions of the distribution of the trees in the area, e.g. *Pterygota* n.sp. is one of the commonest large trees in the area frequented by *Colobus abyssinicus ituricus* but is not so elsewhere.

Occupation of a tree by any species was irregular; sometimes the same species occurred for several nights in succession but mostly only on isolated single nights. In periods 2 and 3 observation was continuous and, neglecting single occurrences and series which began or ended the periods, the percentage of single night occupations among total bands seen for the four main species are as follows:

	%	Bands
<i>Cercocebus albigena johnstoni</i>	73	63
<i>Cercopithecus ascanius schmidtii</i>	76	29
<i>Papio doguera tessellatus</i>	45	36
<i>Colobus abyssinicus ituricus</i>	55	48

The longest series of successive nights occupied for the four species were, respectively, 3, 3, 6, 4.

Table 1 shows that many of the study trees were used by several different species of monkey, but it was only very rarely that two species occupied the same tree on the same night. Among the 749 observations of bands in study trees between 10 August 1948 and 25 March 1949, there were only six occurrences of this sort. Four concerned *Cercopithecus mitis stuhlmanni* which was associated once with *Cercocebus albigena johnstoni*, twice with *Cercopithecus ascanius schmidtii* and once with *Colobus abyssinicus ituricus*. The other two were of *Cercocebus albigena johnstoni* with *Papio doguera tessellatus* and *Colobus abyssinicus ituricus*. Trees nos. 13 and 22 were concerned twice, and nos. 54 and 49 once each. The first three of these trees were of very large size so that the presence of the two species together need not actually imply that they were associated together in a single band. Thus, although mixed species bands may be very frequently seen in the day-time, particularly of *Cercocebus albigena johnstoni* and *Cercopithecus ascanius schmidtii*, it seems definite that segregation at night is almost constantly the rule.

However, in many cases several species of monkey used the same tree on different nights (Table 1). The greatest common use of trees was by *Cercocebus albigena johnstoni* and *Papio doguera tessellatus* and trees nos. 34, 50, 22 and 13, in descending order of importance, were most concerned. These are all trees in the main baboon sleeping area also much frequented by *Cercocebus albigena johnstoni*. The amount of common use of trees was less in the other species pairs but, except perhaps in the case of *Cercopithecus ascanius schmidtii* and *Colobus abyssinicus ituricus*, was still considerable. The four trees most concerned for each species pair were as follows:

<i>P. d. tessellatus</i> — <i>C. a. ituricus</i>	42, 22, 13, 53
<i>C. a. johnstoni</i> — <i>C. a. ituricus</i>	36, 41, 22, 44
<i>C. a. johnstoni</i> — <i>C. a. schmidtii</i>	47, 11, 22, 49
<i>C. a. schmidtii</i> — <i>P. d. tessellatus</i>	22, 54, 11, 13
<i>C. a. schmidtii</i> — <i>C. a. ituricus</i>	22, 42, 54, 41

Tree no. 22 falls among the four most concerned trees in all combinations and tree no. 13 occurs so thrice. These trees are outstanding in their use by several species in succession. They are very large trees, closely adjacent and near the dividing line between the moist and dry forest.

(b) The tracing of an individual band

On 22 September 1948, a record was begun of the number of juveniles in each observed band, it being hoped that by this additional information it might be possible to identify individual sleeping bands. In three of the main species the record is too irregular

to allow anything of this sort, but a band of six *Colobus abyssinicus ituricus* including two juveniles appears frequently in the observations. Further, on many nights when a band of this composition was not recorded an identical constitution may be obtained by adding the records of two or three neighbouring trees. It is believed that these are all the same band and it is worth while to follow its movements in some detail. The nights on which the whole band was identified and its location on those nights are given below. Tree numbers are given in black type and the numbers of juveniles, which are included in the main totals, are given in parentheses. When only the tree number is given all the band were in that single tree.

1948: 22 Sept. 42-4 (2); 48-1; 51-1
 23 Sept. 46
 24 Sept. 42-5 (2); 48-1
 26 Sept. 41
 27 Sept. 41-5 (2); 42-1

No observation: 28 Sept. to 29 Oct. inclusive

1948: 8 Nov. 46
 9 Nov. 41
 10 Nov. 44
 20 Nov. 48-4 (2); 42-2
 24 Nov. 44-5 (2); 41-1
 26 Nov. 23
 4 Dec. 46
 5 Dec. 44
 6 Dec. 36
 8 Dec. 36
 10 Dec. 23
 18 Dec. 42
 19 Dec. 42
 21 Dec. 41-4 (2); 36-2

No observation: 23-27 Dec. inclusive.

1949: 5 Jan. 42-5 (2); 41-1
 6 Jan. 42-5 (2); 41-1
 8 Jan. 36
 9 Jan. 44
 10 Jan. 42
 13 Jan. 41-5 (2); 44-1
 18 Jan. 44-4 (1); 42-2 (1)
 19 Jan. 42-4 (1); 44-2 (1)
 20 Jan. 42
 21 Jan. 46
 22 Jan. 23
 23 Jan. 42
 24 Jan. 23
 26 Jan. 42-5 (2); 51-1
 8 Feb. 41
 13 Feb. 53

Members of the band were recorded from all the trees in Group 5 with the exception of tree no. 28, and all these trees on occasion accommodated the whole band except for trees nos. 48 and 51. Tree no. 51 was occupied twice, on each occasion by single individuals. Tree no. 48 was occupied three times,

twice by single individuals and once by the major portion of the band. Of the total of 35 nights on which the band was located it occupied single trees on 23 nights; it was divided up on 12 nights. Division of the band, therefore, is not unusual and is probably more frequent even than these figures show, as ten further occurrences have been omitted for the reason that all were not located but were probably of the same band. Of the twelve occasions on which the band was divided seven were separations of one, and three of two, adult individuals, and on two occasions the separated pair was of one adult and one juvenile. The major portion of the band occurred in trees nos. 42, 41, 44 and 48, on six, three, two and one occasions respectively. The separation was in all cases over a fairly short distance; the longest was that between trees nos. 41 and 44, which was about 120 m.

This band appears to have been constantly in the area up to 31 January 1949. In addition to the complete findings reported above there were recorded groups which appear to be part of the band and if they are taken into account the longest time in which the band was not observed is only 2 nights. After that date, however, the complete band was only seen twice and possible parts of it only three times. The maximum time lapse over which it was quite unrecognized was 7 nights. As the whole band appeared as late as 13 February and possible components (five monkeys including two juveniles) as late as 20 February it does not appear that the constitution of the band had altered. It is, therefore, probable that the band moved out of the study trees for longer periods in February than previously.

(c) *The size of the night-resting bands*

The distribution of numerical band size (including solitary monkeys) is shown in Table 4 for the several species observed.

Solitary monkeys were recorded for *Cercocebus albigena johnstoni*, *Cercopithecus mitis stuhlmanni*, *Papio doguera tessellatus* and *Colobus abyssinicus ituricus*, but only in the last species were they of very frequent occurrence. Such a result does not necessarily imply that solitary monkeys were not of common occurrence in the species other than *C. a. ituricus*, but only that if they occurred they tended not to use the study trees for sleeping. Solitary *C. a. ituricus* occurred in eleven trees, all of which were also used from time to time by bands, but four trees, numbers 41, 44, 48 and 51, accounted for thirty-two out of the forty-one observations. Tree no. 51 was especially used; eleven out of the thirteen times it was occupied were by solitary monkeys. This tree was a *Xylopia* sp. closely adjoining the rock face; its three separate trunks were unbranched for about 20 m. and carried sparse crowns reaching to nearly 30 m. No such marked predilection for particular trees can be

Table 4. The distribution of numerical band size (including solitary monkeys) for eight monkey species at Mongiro, Bwamba; 10 August 1948 to 21 February 1949

Species	Number of bands with individuals numbering													Totals
	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>C. a. johnstoni</i>	4	17	44	53	28	33	6	4	1	—	—	2	1	193
<i>C. m. stuhlmanni</i>	2	2	3	5	2	—	—	1	—	—	—	—	—	15
<i>C. m. denti</i>	—	—	—	2	—	—	—	—	—	—	—	—	—	2
<i>C. neglectus</i>	—	1	1	—	1	—	1	—	—	—	—	—	—	4
<i>C. a. schmidtii</i>	—	8	11	25	12	11	5	5	2	1	—	1	—	81
<i>P. d. tessellatus</i>	11	18	22	53	30	17	10	10	3	3	—	—	—	177
<i>C. a. ituricus</i>	41	26	24	42	36	48	11	2	2	2	—	—	—	234
<i>P. t. schweinfurthii</i>	—	1	—	—	—	—	—	—	—	—	—	—	—	1

recognized in the small number of records for other species.

If solitary monkeys are omitted, the distribution of numerical band size approximates to normality and the mean band sizes and standard errors for the four species calculated on this assumption are as follows:

<i>Cercocebus albigena johnstoni</i>	4.42 ± 0.13	(189 bands)
<i>Cercopithecus ascanius schmidtii</i>	4.81 ± 0.22	(81 bands)
<i>Papio doguera tessellatus</i>	4.66 ± 0.14	(166 bands)
<i>Colobus abyssinicus ituricus</i>	4.62 ± 0.12	(193 bands)

None of these means differs significantly from one another. The data were also examined for variation in band size in the three successive periods of examination and, where twenty or more bands had been recorded, for variations in the different tree groups. No statistically significant differences were found.

Zuckerman (1932) has recorded, for *Papio comatus* E. Geoffroy, that the band divides for sleeping into small, perhaps family, parties in many separate cliff crevices. The foregoing data are suggestive of a similar condition in these monkey species as the daytime bands seen, at least as far as the four main species are concerned, usually numbered over ten individuals. The modal value (derived by inspection) for all four main species is four with the exception of *Colobus abyssinicus ituricus* in which it is six.

Pan troglodytes schweinfurthii was observed only once. Two adults spent the night of 21 January 1949 in a tree near tree no. 33. They were reported not to have constructed sleeping nests on this occasion.

(d) Seasonal variations in the number of monkeys observed

Before considering this matter any possible artificial factors influencing the results may be considered. There were certain unavoidable disturbances in the area because a road ran through it. These were the passage of natives and occasional vehicles by night. They were, however, roughly uniform throughout the series, as both mainly traversed the area on their ways to regular markets. On 20 nights in the second

period, and 11 nights in the third, evening mosquito catches, which lasted from 15 to 21 hr., were carried out on all five platforms at Mongiro (Fig. 1). Occurrences of monkey bands in the study trees during these catches have been compared with an equivalent number of nights on which there were no catches, as closely related in time as possible. A total of 151 bands of the four main species occurred on 40 nights in the second period, 72 on nights with catches and 79 on undisturbed nights. The corresponding numbers for the third period were 102, 50 and 52. There is, therefore, negligible effect on the total number of bands observed. Study of the effect on separate species in the same data, taking into account all trees in which the species occurred, showed the largest difference in the case of *Papio doguera tessellatus* in the second period. In 220 tree-nights at the time of catches, 15 bands were observed and 21 in 220 tree-nights when catches were in abeyance. This difference is, however, not significant ($\chi^2 = 1.89$ and $P > 0.1$). Where the numbers were sufficient the effects on individual trees were examined. Values of P (derived from χ^2) of less than 0.02 were found for trees nos. 50 and 54 only, and only in the third period when the 11 days of catches were continuous; in the second period the catches were made in groups of five with 2 nights interval. Platforms IV and V are distant only 40–50 m. from tree no. 50; no. 54 is about 100 m. from platform II and 150 m. from the camp used by the mosquito catchers in the third period; there was no camp in the second period. It seems, therefore, that the disturbances which can be assessed had negligible effect on the total population, merely diverting bands to other trees to a small extent.

The effect of weather has also been considered. Period 2, covering the end of the main rainy season, was selected. Twenty-six trees were observed throughout this period, a total of 1378 tree-nights for the 53 nights of observation, of which 17 were immediately preceded by rain. The association was examined for all species together and for the four main species separately. The highest value for χ^2 obtained was 1.68 for *P. d. tessellatus* which, though not statistically

Table 5. *The mean total numbers observed per night of the four main species during five time intervals between 10 August 1948 and 21 February 1949*

Record of monkeys in non-study trees began 7 September 1948, and the value for the first interval was obtained by doubling the value for its second half.

Species	Interval	Number of nights observed	Mean total seen per night		
			Study trees	Other trees	Total
<i>C. a. johnstoni</i>	1 10 Aug. to 27 Sept.	28	5.68	1.86	7.54
	2a 30 Oct. to 24 Nov.	26	4.23	2.62	6.85
	2b 25 Nov. to 22 Dec.	28	6.22	2.82	9.04
	3a 28 Dec. to 24 Jan.	28	6.75	3.68	10.43
	3b 25 Jan. to 21 Feb.	28	6.89	4.68	11.57
<i>C. a. schmidtii</i>	1 10 Aug. to 27 Sept.	28	2.86	0.43	3.29
	2a 30 Oct. to 24 Nov.	26	0.92	0.12	1.04
	2b 25 Nov. to 22 Dec.	28	2.32	1.04	3.36
	3a 28 Dec. to 24 Jan.	28	2.89	2.39	5.28
	3b 25 Jan. to 21 Feb.	28	4.93	2.32	7.25
<i>P. d. tessellatus</i>	1 10 Aug. to 27 Sept.	28	6.75	9.86	16.61
	2a 30 Oct. to 24 Nov.	26	4.85	3.85	8.70
	2b 25 Nov. to 22 Dec.	28	3.96	1.18	5.14
	3a 28 Dec. to 24 Jan.	28	7.57	6.57	14.14
	3b 25 Jan. to 21 Feb.	28	5.22	5.50	10.72
<i>C. a. ituricus</i>	1 10 Aug. to 27 Sept.	28	8.82	3.43	12.25
	2a 30 Oct. to 24 Nov.	26	6.50	3.04	9.54
	2b 25 Nov. to 22 Dec.	28	6.50	1.04	7.54
	3a 28 Dec. to 24 Jan.	28	6.76	1.57	8.33
	3b 25 Jan. to 21 Feb.	28	4.89	1.29	6.18

significant ($P > 0.1$), does indicate that this species is most liable to be affected by rain, and supports the observer's statements that if there is heavy rain just at sunset it does not enter the trees but shelters on the ground.

The factors discussed above have been shown to affect insignificantly the total numbers of monkey bands observed in the area and therefore may be neglected in a consideration of seasonal variations. On 7 September 1948, a record was begun of the monkey bands seen in other than study trees. Table 5 is based on these data as well as those from the study trees, and shows the mean nightly numbers of monkeys seen in both categories of trees, and their totals, for five intervals of which the first is identical with the first period and the rest are halves of the second and third periods. The record of monkey bands in non-study trees began in the middle of the first interval and the value for this was obtained by doubling the observations of its second half. Fig. 4 shows the data graphically and also gives the maximum numbers seen in any one night for each interval.

The highest number seen in any one night may be taken as giving an indication of the total population in the area during any given interval. If these values are compared with the mean numbers seen per single night it appears that in the cases of *Cercocebus albigena johnstoni* and *Colobus abyssinicus ituricus* about half the population were located each night. The proportion was, however, much lower for *Cercopithecus*

ascanius schmidtii and *Papio doguera tessellatus*, being only about a quarter. It is difficult to explain the variations shown in Fig. 4 except as variations in the total population. Various possible influencing factors have already been eliminated. The conditions for observations were not at all variable through the series; the forest is mainly evergreen and visibility in it was not subject to any appreciable variation in this respect, and even if this were so the effects would be expected to be parallel in all species. This consideration would apply also to variations in the acuity of the observers. It seems, therefore, that the population of *Cercocebus albigena johnstoni* and of *Cercopithecus ascanius schmidtii*, though both species suffered some reduction in the first half of the second period, in general increased through the observation series. This finding agrees with day-time observations, at least as far as *Cercocebus albigena johnstoni* is concerned, as it was noticed to be extremely abundant in the area in February and March 1949. The numbers of *Papio doguera tessellatus* are erratic. *Colobus abyssinicus ituricus* decreased nearly regularly through the series. These variations are almost certainly to be explained by migration in and out of the area and as this was small, migrations over quite small distances could give this effect. Probably such movements are connected with variations in the distribution of the preferred food supplies. *C. a. ituricus* feeds mainly on the evergreen *Cynometra alexandri* (Haddow, Smithburn, Mahaffy & Bugher, 1947) which is constantly avail-

able, but perhaps the water content of the leaves is insufficient in dry weather—the leaves of many plants lose turgor during the day in the dry season in Bwamba.

Besides the 15 bands of *Cercopithecus mitis stuhlmanni* recorded above there were two more whose number was unknown and therefore were not considered there. Of the total of 17 bands, 2 occurred in the first period, 4 in the second, and 11 in the third. On this small number of examples it seems that the species is more common in the area in the dry season and not, as Haddow, Smithburn, Mahaffy & Bugher (1947) state, in the wetter weather. The two bands of *Cercopithecus mona denti* seen were one each in the first and second periods. Three of the four *C. neglectus* bands occurred in the second period and the other in the third.

(e) *The times of entering and leaving the sleeping trees*

It is convenient, before dealing with data from observations on wild monkeys, to deal with those from captives. Two *Cercopithecus ascanius schmidtii* were available, one being a sub-adult male and the other a juvenile female. They were observed for a minute every quarter of an hour from 05.15 to 19.00 hr. on 2 days and their main and subsidiary activities noted. The first day was mainly sunny with cloudy intervals, the second was mainly cloudy; the maximum shade temperatures in the 2 days were, respectively, 33.2 and 29.0° C. On the basis of the recorded main activity an activity rating was allotted to each monkey at each observation. The scale used was as follows:

- Rating 0. Sleeping or sitting still.
- Rating 1. Sitting activities, e.g. grooming, feeding, etc.
- Rating 2. Walking or quiet play.
- Rating 3. Running or active play.
- Rating 4. Very active play; jumping.

The observations for both monkeys and both days have been combined by successive pairs and are shown in Fig. 5.

Activity shows two main maxima, the first immediately after it begins in the morning and the second a little before it ends in the evening. The first was the more marked, and, especially in the male, consisted of a series of bouts, each lasting about 20 sec. with shorter intervals, of extraordinarily vigorous jumping. The series lasted from about 05.40 to 06.10 hr. except for a few subsequent bouts. It was followed by a period of less active but still vigorous play which lasted till about 08.30 hr. The second maximum was similar. The first maximum was reached before sunrise but the second ended considerably before sunset. The period of lower activity in the middle of the day was roughly co-extensive with that of maximum or near-maximum temperatures. On the hotter day both monkeys slept for short periods between 12.45 and 13.15 hr. Food was brought at 08.30 hr. daily

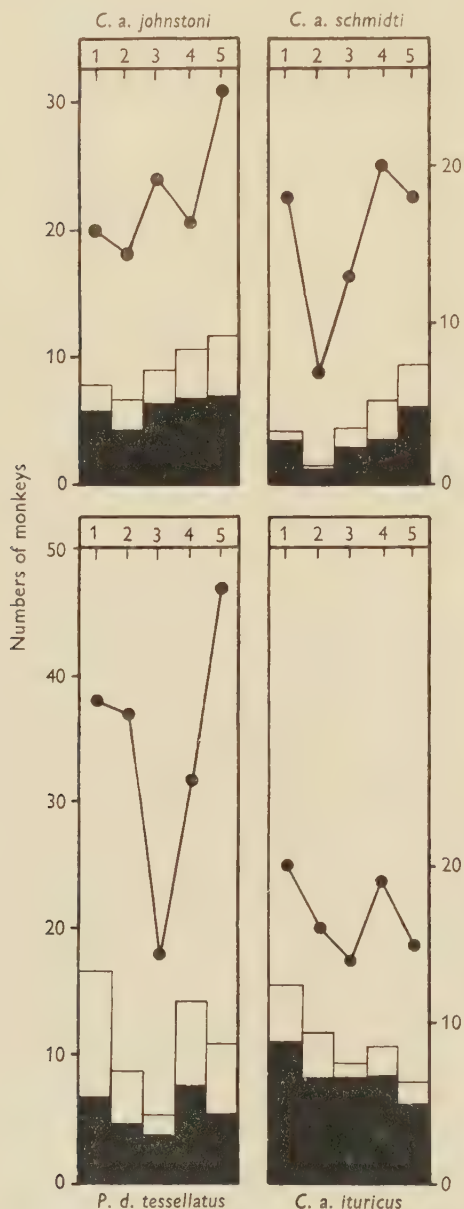


Fig. 4. Mean total numbers of the four main monkey species observed per night in five intervals between 10 August 1948, and 21 February 1949 (histograms); from data of Table 5. Contribution of study trees black, of non-study trees, white. The maximum numbers seen on any single night in each interval are also shown (curve).

but some remained from one day to another, and some feeding occurred at every time of observation between 06.00 and 16.45 hr.

Table 6 shows the total recorded inactive monkeys in a series of seven trees (trees nos. 11, 13, 22, 34, 36, 42 and 50) which were observed from 1 to 25 March 1949, by 10 min. periods from 05.30 to 07.00 at dawn and 17.00 to 18.30 at dusk. Besides those monkeys which were recorded in a series of successive periods ending or beginning at dark and which therefore

and *Colobus abyssinicus ituricus* leaving may have begun before observations began, as the first dawn period totals are less than those of the last dusk period; however, this may simply be due to the difficult conditions for observation in the first dawn period. *C. a. ituricus* which entered the trees earlier at dusk tended to leave them later at dawn; by period 5, when all the *Cercocebus albigena johnstoni* and *Papio doguera tessellatus* had left, 28 % still remained on the trees.

The trees for this series of observations were chosen

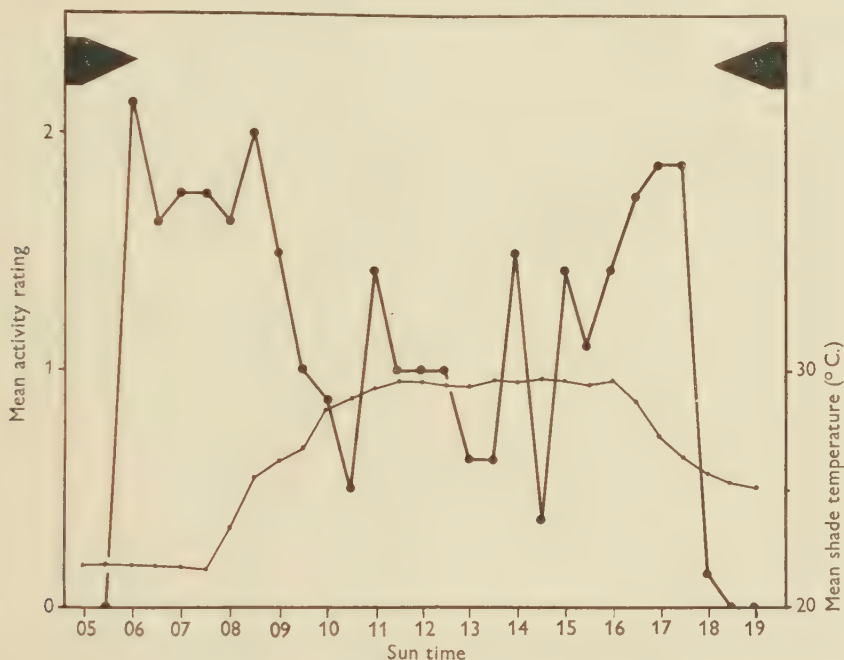


Fig. 5. The diurnal rhythm of activity of captive *Cercopithecus ascanius schmidtii* (large dots); based on 2 days' observation of two specimens at 15 min. intervals together with the mean shade temperatures (small dots). For method of study see text. The periods of transition between sunrise or sunset and darkness (astronomical twilight) are shown by wedges.

nearly certainly spent the night in the trees, there were also inactive monkeys which left before, or appeared after, dark. These have been separated in Table 6 (A and B). Fig. 6 shows the percentage, period by period, which had entered, or which remained on, the trees at dusk and dawn respectively for three of the four main species. All or almost all monkeys of the three species were in the trees by period 7 which immediately follows sunset, but there are considerable differences in the rates of attaining complete settling. *Papio doguera tessellatus* was latest, only 8 % being inactive in period 4, by which time 35 % of the *Cercocebus albigena johnstoni* had settled and 55 % of the *Colobus abyssinicus ituricus*. At dawn all three species begin to leave after the first observation period. In *Cercocebus albigena johnstoni*

as those most likely to yield timed observations on all four main monkey species. It was unfortunate that during the series *Cercopithecus ascanius schmidtii* did not occur, as thereby comparison of observations in the wild with those on captive monkeys of the same species is precluded. However, the curves for the captive redtails agree essentially with the findings for the three species which did occur. The early onset of activity in the morning at about 20 min. before sunrise and the cessation in the evening about sunset agree closely. It should be pointed out that *Papio doguera tessellatus* which settles latest of the three species observed was also one of the four main species in which it appeared that only about a quarter of the population was located on an average (see earlier). The observers reported that *Cercopithecus ascanius*

Table 6. The total numbers of inactive monkeys on seven trees (nos. 11, 13, 22, 34, 36, 42 and 50) between 05.30 and 07.30 and between 17.00 and 18.30 hr. by nine 10 min. periods; 1-25 March 1949

A: monkeys spending the night on the tree. B: monkeys leaving before or arriving after dark.

		Number of 10 min. period and its time of beginning																	
		Dusk									Dawn								
Part	Species	(1) 17:00	(2) 17:10	(3) 17:20	(4) 17:30	(5) 17:40	(6) 17:50	(7) 18:00	(8) 18:10	(9) 18:20	(1) 05:30	(2) 05:40	(3) 05:50	(4) 06:00	(5) 06:10	(6) 06:20	(7) 06:30	(8) 06:40	(9) 06:50
A	<i>C. a. johnstoni</i>	4	5	10	17	28	40	48	48	48	42	28	14	2	—	—	—	—	—
	<i>P. d. tessellatus</i>	—	—	—	4	13	26	46	46	49	49	33	14	2	—	—	—	—	—
	<i>C. a. ituricus</i>	7	10	20	22	28	29	40	40	40	36	24	20	18	10	5	2	1	1
B	<i>C. a. johnstoni</i>	2	1	10	3	—	2	—	—	—	—	2	3	3	26	18	6	2	2
	<i>C. neglectus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—
	<i>C. a. schmidtii</i>	—	—	—	—	3	2	—	—	—	—	—	—	3	2	—	—	—	—
	<i>P. d. tessellatus</i>	2	2	3	4	1	—	1	—	—	3	1	4	5	1	—	—	—	—
	<i>C. a. ituricus</i>	7	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3

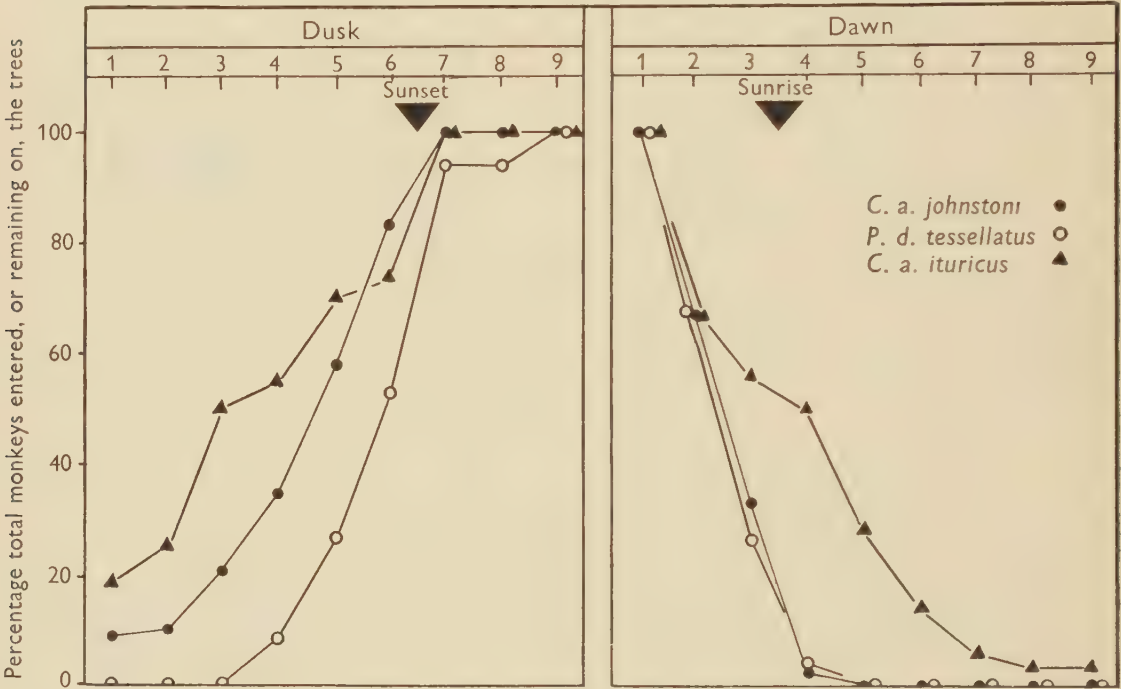


Fig. 6. The percentages of the total population entered, or remaining on, the sleeping trees by nine 10 min. periods at dawn and dusk for three species; from data of Table 6. Based on 25 nights observation of seven trees.

schmidtii, which also was located only to a small extent, tended to come into the trees even later than did *Papio doguera tessellatus*. It is probable that many occurrences of these species were missed on this account.

Five species were recorded as spending some time inactive in the trees but arriving after or leaving before, dark (Table 6, B). The numbers, however, are small except in the case of *Cercocebus albigena johnstoni*. This species occurred in considerable numbers in the third dusk period and in the fifth and sixth dawn periods. Their leaving the sleeping trees in the evening before dark may perhaps be due to their diversion by

the observer; but the morning occurrence cannot be explained on this ground, as the monkeys are leaving the trees in any case at this time. It seems, therefore, that *C. a. johnstoni* may enter the trees from other perches after daylight and remain for short periods before again leaving. The *Colobus abyssinicus ituricus* occurring in the first and second dusk periods were apparently displaced by a band of *Cercocebus albigena johnstoni* which came in in the second period and stayed thereafter.

Acting on the observation that captive redtails may sleep for short periods at mid-day, the seven trees in this series were also watched for inactive monkeys

between 12.30 and 13.30 hr. During 25 days' observation of the seven trees in this manner a total of 10 *Colobus abyssinicus ituricus* were seen on three occasions (trees nos. 11 and 13), and a single *Cercocebus albigena johnstoni* (tree no. 22). None of these trees was very highly preferred by the species concerned for night resting. It appears, therefore, that if wild monkeys have a similar habit they do not return for it to the most preferred night trees.

(f) Other observations

With the exception of *Cercopithecus neglectus* and *Pan troglodytes schweinfurthii* all the species reported have been seen by the writer in the area and some of the night-resting behaviour of all four main species, though particularly of *Papio doguera tessellatus* and *Colobus abyssinicus ituricus*, was observed in the course of twenty personal visits, either at dawn or at dusk, to check the work. No personal observation disagrees with conclusions deduced from the record of the observers, but a few additional points may be added.

Cercocebus albigena johnstoni and *Colobus abyssinicus ituricus* sleep among small branches on the periphery of the crown of the tree. The twigs in the centre of the top of tree no. 33, that most preferred by *Cercocebus albigena johnstoni*, were on this account almost leafless. *Colobus abyssinicus ituricus* prefers usually small branches outstanding from the main crown either above it or at its sides. This habit has also been observed by Haddow (personal communication). *Cercopithecus ascanius schmidtii* was reported also to sleep usually among small twigs. On the other hand, *Papio doguera tessellatus* prefers large horizontal, or nearly horizontal, branches near the main tree forks and therefore at a lower average level than the preceding species.

Although *Colobus abyssinicus ituricus* comes into the trees earlier than *Cercocebus albigena johnstoni* and *Papio doguera tessellatus* the monkeys do not take up their actual sleeping positions till about sunset. Generally they occupy positions in the lower part of the crown at first, sometimes moving short distances among the lower, larger limbs. At this time some may rest prone on large branches with their limbs hanging down on each side of it, but usually they sit. At about sunset, however, they move to the top sides of the crown and take up their positions for the night. In the morning some bands may leave the trees completely when they start to move, while some monkeys of other bands may remain till very late. For example, on one morning a band of seven left tree no. 36 completely at 06.11 hr., while a band of six including two juveniles in tree no. 42 had not moved at all till 06.18 hr. At this time a single monkey, from its size apparently a male, moved out of the tree, and a second, also apparently a male, at 07.08 hr. The remaining four

monkeys, two females each with a single juvenile, remained in the tree, the last not leaving until 08.40 hr. The band of six individuals was that whose movements were traced in detail above and the present observation suggests that its constitution was of two adult males, two adult females and two juveniles. Both these juveniles were small and probably still being suckled. It seems probable, therefore, that the separations of single adults were of a male, those of two adults were two males and those of an adult and a juvenile were of a female and its juvenile.

In the daytime *P. d. tessellatus* was frequently seen in a band numbering about 40 individuals but also in smaller ones of only 16 to 20. The sleeping parties apparently separate from the band in succession at about sunset. For example, on one occasion a band, from its volume of vocal sound apparently of large size, approached tree no. 34 and continued past it. However, as it passed three monkeys separated from the band, one taking up a sleeping position in tree no. 34 and the other two in another tree nearby. The vocal sound of the main band continued for about another 5 min. but the separated individuals kept complete silence.

7. DISCUSSION

The five platforms at Mongiro which have been used in recent studies on biting insects in the forest canopy are all in the *Mitragyna stipulosa* forest; four of them are marked on Fig. 1. The platforms, being constructed in the trees themselves, are of necessity in strong forks and are therefore in the middle or lower part of the tree crown. From the present work it appears that the catch on these platforms is probably very closely representative of the fauna attacking *Papio doguera tessellatus*, as this species rests at night mainly in the swamp forest and also on the lower larger branches of the trees. The biting fauna obtained probably approximates less closely to that attacking *Cercocebus albigena johnstoni* which prefers the top of the crown, though the differences in this case are likely to be only quantitative rather than qualitative. In the case of *Colobus abyssinicus ituricus*, however, and to a lesser extent *Cercopithecus ascanius schmidtii*, the most used sleeping places are in an environment rather different from that sampled by the present mosquito catch platforms. Most of the located sleeping positions of these species were in the dry forest, those of *Colobus abyssinicus ituricus* exposed on the outside of the crowns of the bigger trees at levels much above that of the extant platforms.

The normally used bait in mosquito studies of three native children probably approximates closely in attractiveness to biting insects to the most usual monkey sleeping party, of four individuals.

As far as time of entering the sleeping trees is concerned, *Cercocebus albigena johnstoni*, *Papio doguera tessellatus* and *Colobus abyssinicus ituricus* are all likely to be heavily attacked by *Aedes* (*Stegomyia*) *africanus*. This mosquito exhibits its maximum biting activity in the forest canopy at 18.00–19.00 hr. (Haddow, Gillett & Highton, 1947), at which time the present study shows all these three species are settled in their trees.

None of the trees studied was confined to use by a single monkey species, and most were occupied by several in succession. It is not impossible, therefore, that a condition of endemic yellow fever could be produced in the whole monkey population by bites of arthropods of short range, each monkey species being infected in turn as a given tree was occupied. Some evidence in the present work indicates that the numbers of some species in the area are subject to fluctuation, probably due to migrations, though these may be of only small extent. Such migrations might be of importance in the dissemination of yellow fever virus in the forest, but the succession of different monkey species in any given tree could effectively perform the same function. The several species are of different habits and probably compete to a negligible extent; the territories of bands of different species are therefore unlikely to have identical boundaries, the boundary between the band territories of any given species being overlapped by the territory of another.

8. ACKNOWLEDGEMENTS

I am deeply indebted to Dr A. J. Haddow whose wide knowledge of African monkeys has been put freely at my disposal in discussion. To Dr S. F. Kitchen for assistance in preparation of the paper and to Drs W. J. Eggeling and I. R. Dale, of the Uganda Forest

Department, for help in the identification of tree specimens, I am also most grateful.

9. SUMMARY

1. The results are reported of a series of observations on monkey-sleeping trees in a small area in the Semliki Forest, Uganda, from January 1948 to March 1949. Eight species of monkeys occurred in the area (see § 4, p. 15).

2. The trees are divided into five groups on topographical and botanical bases and the preference of the various monkey species studied for each as well as for individual trees.

3. Occupation of a single tree by more than one species in the same night was unusual, but several species used any given tree on different nights.

4. The movements of an individual band of *Colobus abyssinicus ituricus* (Lowland colobus) are discussed.

5. The sizes of the night resting bands are studied and it is concluded that they are fragments of the diurnal bands.

6. Some evidence is produced of population changes in the area, probably due to migrations, though these may be only over short distances.

7. Some observations on the diurnal activity rhythm of captive monkeys are reported and they are compared with timed observations on the settling into, and leaving from, the night resting trees, of three species in the wild. *C. a. ituricus*, *Cercocebus albigena johnstoni* (Black mangabey) and *Papio doguera tessellatus* (Anubis baboon) settled in that order in the evening and *Colobus abyssinicus ituricus* tended to remain later in the morning than the other two species.

8. The parts of the trees used for resting by the main species of monkey are discussed.

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FURTHER OBSERVATIONS OF THE NIGHT-RESTING HABITS OF MONKEYS IN A SMALL AREA ON THE EDGE OF THE SEMLIKI FOREST, UGANDA

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1. INTRODUCTION

Lumsden (1951) carried out a thorough study of the sleeping habits of the monkey population living at Mongiro, on the edge of the Semliki Forest, in Bwamba County, Western Uganda. He used African observers, under the charge of a reliable African supervisor, to record the trees in which inactive monkeys were seen at dusk and dawn. The trees were numbered with metal tags nailed to the trunk.

The present writer visited the same area on 4, 6 and 7 July, 1950, in company with the same African supervisor, and the most experienced observer. Many of the trees still bore the numbered tags. Those that had lost their tags were readily recognized by one or both of the Africans, and the identifications were checked by referring to Lumsden's map.

Reference should be made to the previous paper for information on the monkeys, and a detailed description of the area. Individual trees are referred to below by the numbers used by Lumsden.

The only species of monkey seen to occupy numbered trees during the 3 nights of observation were *Colobus abyssinicus ituricus* Matschie (Lowland colobus), *Papio doguera tessellatus* Elliot (Anubis baboon) and *Cercocebus albigena johnstoni* Lydekker (Black mangabey).

2. OBSERVATIONS

All observations, which were made at dusk only, were recorded by the supervisor. Most of them were confirmed by the writer.

The results are given in Table 1.

The following trees were observed to be unoccupied each night: nos. 25, 19, 28, 44, 46, 23, 30, 48, 51, 53, 52 and 27. The majority of the remainder were observed to be unoccupied on at least 1 of the 3 nights of observation, but no detailed records were kept. The southern part of the area had recently been considerably disturbed by tree felling, and the manufacture of dug-out canoes from the felled tree *in situ*. Trees

nos. 54 and 33 had recently been felled. It is possible that this disturbance accounts for the fact that no inactive monkeys were observed at dusk or dawn in Lumsden's tree groups 2 or 3, though active monkeys were seen in these areas in daylight.

Table 1. *Trees (numbered as in Lumsden (1951)) occupied at dusk on 4, 6 and 7 July 1950, the monkeys occupying them, and their order of importance for all species as observed by Lumsden (1951)*

Tree no.	4. vii. 50	6. vii. 50	7. vii. 50	Order of importance given in Lumsden (1951)
29	4 <i>Colobus</i>	—	—	—
42	—	1 <i>Colobus</i>	1 <i>Colobus</i>	4th
41	—	4 <i>Colobus</i>	4 <i>Colobus</i>	8th
36	4 <i>Colobus</i>	4 <i>Colobus</i>	3 <i>Colobus</i>	6th
7	—	6 <i>Papio</i>	3 <i>Cercocebus</i>	14th
22	—	2 <i>Papio</i>	—	3rd
13	—	3 <i>Papio</i>	6 <i>Papio</i>	5th
34	—	—	8 <i>Papio</i>	1st

From Lumsden's paper it is apparent that trees nos. 7, 13 and 22 were first observed to be sleeping trees during the first week of February 1948, and that trees nos. 29, 34, 36, 41 and 42 were recorded before 18 March 1948. The present observations show that the same trees were still in use after nearly 2½ years.

Dr A. J. Haddow (personal communication) states that as long ago as December 1944, tree no. 33 was in use as a sleeping tree by *C. a. johnstoni*, and trees nos. 13 and 22 by *Papio doguera tessellatus*. There is no reason to doubt that the trees noted by Haddow were in fact these trees, as they are all large and conspicuous. Dr Haddow also states that two trees in the adjacent forest of Mamirimiri were frequently used as sleeping trees by *Cercocebus albigena johnstoni* from June 1944 to July 1948.

It is seen from a study of Table 2 in Lumsden's paper that at least some of the trees more important during his study are still in constant use. The last column of Table 1 in the present paper gives the order of frequency in which the trees were used by the four most important monkey species during

* This Institute is financed by means of grants by the Secretary of State for the Colonies under the Colonial Development and Welfare Acts and by contributions from the Governments of Uganda, Kenya, Tanganyika Territory, Northern Rhodesia, Nyasaland and Zanzibar.

Lumsden's study. Lumsden's Table 2 also gives the order of importance for each tree for each species. In the present study *Colobus abyssinicus ituricus* was seen in trees nos. 42, 36 and 41 which were previously first, second and fourth in importance respectively. This species was also seen in tree no. 29 which, in the former study, was not an important tree. Similarly, *Papio doguera tessellatus* was seen in trees nos. 34, 22, 13 and 7 which were previously first, third, fourth and fifth in importance. Tree no. 7 was seventh in importance for *Cercocebus albigena johnstoni*.

3. DISCUSSION

The duration of time during which the habits of the monkeys of an area remain constant is of interest. Haddow, Dick, Lumsden & Smithburn (1951) give evidence to show that most monkeys live for a period of 10 years, and some up to 20 years. Lumsden (1951) gives evidence to show that sleeping bands are family units.

The present series of observations show that the habits of each species in a small area of forest have remained constant for several years, the maximum period from the first observations to the present series being $5\frac{1}{2}$ years.

Causey, Laemmert & Hayes (1948), working in

Brazil on *Cebus* monkeys, found that during a trapping and marking experiment lasting over 15 months individual monkeys did not move away from quite small areas, and that bands of monkeys occupied territories. The writer, during current work in Uganda on the redtail monkey (*Cercopithecus ascanius schmidtii* Matschie), has found no evidence of territory, though the daily habits of troops are fairly constant (unpublished results).

From the evidence given above it is possible that some of the individual monkeys observed by Haddow in December 1944, are the same as those observed by the writer in July 1950. The habits of a family group may remain constant for a period longer than the life-span of the individual.

4. ACKNOWLEDGEMENTS

My thanks are due to Dr W. H. R. Lumsden, and to Dr A. J. Haddow for considerable help and advice.

5. SUMMARY

Evidence is presented to show that over a period of $5\frac{1}{2}$ years some of the monkeys of Mongiro Forest, Bwamba County, Uganda, have used the same individual trees as night resting places.

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THE ECOLOGY AND DISTRIBUTION OF BLACK-FLIES (SIMULIIDAE) IN SOUTH-EAST SCOTLAND

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(With Plates 1-5 and 2 Figures in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	33	4. GENERAL BIOLOGY	55
2. MATERIAL AND METHODS OF STUDY	34	(a) Hibernation	55
3. DISTRIBUTION OF <i>SIMULIUM</i> SPECIES IN		(b) Generations	56
SCOTTISH STREAMS	38	(c) Economic position of the Simuliidae	58
(a) Habitat factors	38	5. ACKNOWLEDGEMENTS	60
(b) Species composition of the different waters	44	6. SUMMARY	60
(c) Notes on species and their association	48	REFERENCES	61

1. INTRODUCTION

The first to look into the problem of the distribution and ecology of black-flies in Britain was Edwards (1915, 1920). Smart (1936), in a paper on the Simuliidae of Fortingal, Perthshire, furnished a foundation for the distribution of the species in that locality. Recently in England the effect of the chemical composition of stream water on the immature stages of *Simulium* was considered by Pentelov (1935), and by Butcher, Longwell & Pentelov (1937) in a survey of the non-tidal reaches of the River Tees.

In the summer of 1945 we started collections and observations by way of a preliminary investigation. In 1946 an extensive programme was carried out in the south-east of Scotland, and the following streams and localities were chosen for regular observations.

(1) Water of Leith: five localities between Harperrig and Slateford, Midlothian. Two further localities on this stream were also occasionally examined.

(2) Murrieston Water: two localities between Nether Williamston and Midcalder, Midlothian.

(3) Linhouse Water: three localities between Crosswood and Midcalder, Midlothian. The River Almond, into which Linhouse Water flows, was occasionally examined.

(4) East Bavelaw, a stream flowing into Threipmuir Reservoir, Midlothian.

(5) North Esk River: five localities between its source on the Pentland Hills and Musselburgh, Midlothian.

(6) Fingland Burn and a tributary (a small mill lade), Traquair, Peeblesshire.

(7) Certain localities on the Whiteadder, Blackadder and tributaries were examined in midsummer 1946 and again later in the season.

In addition, many other streams were examined occasionally, and in September 1946 the survey was extended north and west to Stirlingshire, Perthshire, Aberdeenshire, Banff, Moray, Inverness-shire, Argyllshire and Dumbartonshire.

Tables 10, 11 list all streams and localities in which the investigation was carried out.

During each field excursion notes were made on the presence and relative abundance of *Simulium*, the characters of the stream bed, rate of current flow, temperature of the water and other relevant data. Representative samples of the immature stages of black-flies and of the associated fauna and flora were taken, and chemical analyses were made of samples of water taken from different streams.

After obtaining a considerable knowledge of the species distribution, it was found necessary to make a close study of larval habitats with a view to ascertaining the optimum conditions required by the immature stages of *Simulium*. In addition, a check was kept on the results obtained from the 1945 and 1946 surveys, particularly those referring to aspects of distribution. In 1947, four streams were chosen for this special part of the investigation: Water of Leith, Blackadder, Whiteadder and Fingland Burn. Another stream was added later, Westquarter Burn, Laurieston, Stirlingshire, after the discovery of *S. ornatum* attacking cattle and horses in the vicinity of the Burn. At these streams sixteen localities were chosen, based on records obtained from our 1946 survey, representing upland, semi-upland and lowland areas; and periodic visits were paid at about monthly intervals. In addition, some other districts were visited, each on one occasion in 1947.

Two prime difficulties faced us in this investigation. The first was the wide range of variation in the larvae,

which made the ready distinction of species far from easy. Papers of Edwards (1915, 1920), Puri (1925) and Smart (1944), which deal in great detail with the morphological features of the immature stages, do not envisage the many variations which may occur even in a population taken from a single site, such as a leaf or a stone. Hundreds of samples and thousands of larvae were collected and examined during the course of the investigation, and it was finally possible, after inspection of a wealth of material, to distinguish species with considerable ease. The pupae, as contrasted with the larvae, were found to be more uniform in character and thus easier to identify, and identification of species was often confirmed where possible by rearing adults from collected pupae stored in Petri dishes.

The second difficulty was to estimate the density of larval populations in view of the mobility of these organisms in their extensive habitats. In 1946, the records of low, moderate and high densities were obtained by personal observation, but it was necessary to discover a more accurate method of computing the density. One, designated the 'time method', proved impracticable and the other, referred to as 'site observations', inaccurate (see p. 35).

In the course of this investigation we have paid about 350 visits to nearly a hundred localities in different parts of Scotland. Ten species were encountered: *S. ornatum* Meigen, *S. monticola* Friederichs, *S. variegatum* Meigen, *S. latipes* (Meigen), *S. reptans* (L.), *S. tuberosum* Lundstroem, *S. aureum* Fries, *S. equinum* (L.), *S. venustum* Say and *S. nölteri* Friederichs.

Of authors who have studied *Simulium* abroad, Pomeroy (1916) made a very useful contribution to our knowledge. His ecological and biological study, though concise, provided important information in many directions. When the present investigation was well advanced in 1947, we were enabled, through the kindness of Dr J. Smart, to consult some of the Russian literature, including papers by Stukolkina (1939) and Rubzov (1939*a, b*, 1940). Certain more recent relevant publications by French authors, e.g. Grenier (1944, 1945*a, b*) became available in 1947.

All attempts to collect adults of *Simulium* in the field by sweeping grass, heather, reeds, bushes and trees in the vicinity of streams known to be densely populated by the immature stages, proved negative. It was only in June 1947, through Dr A. E. Cameron's advice, that a farmer at Laurieston, Stirlingshire, Mr S. Smith, who knew the flies and had observed their attacks on his cattle, was consulted. On his farm it was possible to make observations on living adults of *S. ornatum* and to examine an adjacent stream where breeding had previously been discovered by Cameron (1945).

2. MATERIALS AND METHODS OF STUDY

Collections of the immature stages of *Simulium* can be readily made by removing from streams the stones and leaves to which they are attached (Smart, 1934*a, b*). In 1946, it was planned to define the habitat of *Simulium* by the recording of the following features of streams in which species occurred: the geography and topography of the locality, the width of the stream, the kind of vegetation on which *Simulium* larvae were found, type of stream bed and the presence of moss and algae, type of current, velocity of the flow and water-level. With regard to the stages of *Simulium*, the following categories were recognized:

- (1) Small larvae; 1st, 2nd and 3rd instars.
- (2) Intermediate larvae; 4th and 5th instars.
- (3) Mature larvae; final instars.
- (4) Pupae.
- (5) Empty pupal skins and cocoons.

Segregation of the larval instars into size-groups is not an easy matter by reason of their great variation. In a single sample taken from one site, larvae of as many as ten different sizes could be recognized.

At the outset of this investigation, the density of population was determined by the comparative abundance or scarcity of larvae and pupae collected from stones and vegetation, and roughly estimated by the ease or difficulty experienced in obtaining the sample. In one stream a handful of vegetation taken might produce thousands of larvae and pupae, while in another stream very few might be obtained. The same variation applies to water-washed stones. Time must be considered a factor in estimating the density of population, since the time spent in obtaining a measured sample may to some extent be considered an index of the density. A trial was made at the beginning of December 1946, at Crosswood Burn where the population was low; the time taken to search for and recover the larvae on stones and vegetation was recorded. In a stretch of 50 yd. of the stream (width about 3 yd.), 194 larvae were collected, while in another 50 yd. the count was 86 larvae, each collection occupying 15 min. By contrast, collections from the Water of Leith, Haugh Head or Blackadder Water, Nisbet Hill, in midsummer gave counts of thousands of larvae and pupae from stretches of 1 yd. in less than 2-3 min. Again, one stone of nearly 20 sq. in. in the Fingland Burn, Traquair, in the spring, and another in the Whiteadder in the summer of 1946, gave counts of about 3000 larvae (*S. variegatum* and *S. monticola*) and about 6000 larvae and pupae (*S. reptans*, *S. variegatum* and *S. ornatum*) respectively. The time method, however, was shown to be impracticable since no true comparison could be made between streams differing in width and nature of substrata, not to mention lack of uniformity of size in the various larval instars.

In 1946, estimation of population densities was based on personal observations of the frequency of colonized stones and vegetation at selected sites and the extent of the colonies discovered.

For the more intensive study of 1947, it was decided to find, if possible, a more satisfactory method than that of time for determining the density of larval-pupal populations. An experiment was made with white glazed tiles 6 in. square sunk in a stream bed at places where the effect of different currents and other conditions on *Simulium* populations could be investigated. Soon after being placed in position at suitable sites, the tiles become colonized by larvae. The number of tiles laid at any one site was determined by the width of the stream channel, one tile per $1-1\frac{1}{2}$ yd. Thus, three tiles were arranged at equal intervals across a stream 3-5 yd. wide, and held in position by a frame of wire. Counts of larvae and pupae attached to the tiles were made at monthly intervals, when they were raised close to the surface of the water in order to facilitate counting.

Several sets of tiles were placed in position in May 1947 at sites chosen in the Water of Leith, Langton Burn, Blackadder Water and the Whiteadder. Unfortunately the experiment did not yield satisfactory results since the tiles were apt to become silted over and coated with algae and vegetable debris, which apparently rendered their surfaces unsuitable for larval attachment. Further, in flood waters the tiles were liable to be washed away, and at periods of low water to be left high and dry and were thus abandoned by any larvae they had previously acquired.

The tile method might have proved more satisfactory had it been possible to attend to them more regularly, twice per week instead of monthly, to remove accumulated sediment and debris.

Finally, it was decided to concentrate on certain chosen sites with a view to correlating population density with such factors as type of vegetation and rate of current, as in the case of implanted tiles. Here, estimation of the population was based on measured samples of larval substrata taken from the stream beds and vegetation. In any particular locality three or five sampling sites were selected in a stretch of 100-200 yd. of the stream, representing as many conditions as possible associated with speed of current, character of bed, stony or otherwise, and macroflora. The spacing of the sites was deemed of no importance. At each site three stations A, B at the edge and C in the middle were considered and the sites 1, 2, 3, etc. were marked by wooden stakes. Site 1 was located upstream and the others in order downstream from it. At each site records were made of the salient environmental characteristics. At stations A and B at the stream margins where vegetation occurred, the following features were noted:

(1) Distribution of vegetation and its density, whether patchy or uniform.

(2) Specific composition of vegetation, including the various species of plants present and whether colonized by *Simulium*.

(3) Type of vegetation, trailing, floating or submerged.

(4) Condition of vegetation, green brown or decaying.

(5) Presence of algae, moss and sediment on vegetation.

(6) Presence and density of *Simulium* population.

Sampling of vegetation for Simulium

For estimating the density of the population at any one site a standard sample of the vegetation covering 1 sq.ft. was taken from each edge. If, however, an initial examination showed that there was considerable variation in the larval population, two or three smaller samples were extracted. In all cases, the amount of foliage taken on each occasion was sufficient to fill a jar of 16 oz. capacity. The samples were later examined and counted in the laboratory. It should be emphasized that a locality in which five sites on each bank were established should yield ten samples per visit. Streams which have sites deficient in vegetation or *Simulium* population yield fewer samples. According to the number and the size of samples obtained during the whole period of observations, an approximate estimation of the population density of each locality could be drawn as shown in Table 1.

As regards the stream bed (C), the following characters were noted at the time of sampling:

(1) Type of stream bed, whether muddy, gravelly or stony and presence or absence of vegetation.

(2) Size of stones; the average size was recorded as well as the maximum and minimum sizes.

(3) Condition of stones, whether exposed or submerged.

(4) Surface of stones, whether rough or smooth, clean or coated. The presence of moss, algae and sediment was also recorded.

Examination of stones for Simulium

Here a standard examination was made of ten water-washed stones taken at random and, after careful search, the number of colonized stones recorded and the larval population was estimated as low, moderate or dense according to the degree of uniformity of larval distribution on individual stones and more precisely the number of larvae present per square inch. A summary of the results is given in Table 2.

In all cases the type of current, its velocity and the water-level were recorded. A record of the presence

Table 1. Observations at chosen sites (May to September 1947)

Stream	(Samples from 1 sq.ft. of vegetation)							Total samples obtained	No. of sites, on both banks A and B	No. of visits	Density
	Frequency distribution of <i>Simulium</i> larvae in samples										
	Below 50	51-	201-	501-	1001-	1501-	> 2000				
Water of Leith,											
Upper Harperrig	7	5	2	1	.	.	.	15	10	3	Few
Lower Harperrig	17	3	2	.	.	.	.	22	10	5	Few
Haugh Head	9	12	10	6	2	2	2	43	10	5	Abundant
Balerno	6	3	1	.	.	.	.	10	6	5	Few
Slateford	8	.	.	.	.	.	.	8	6	4	Rare
Cockburn,											
Listonshiels	2	3	3	.	2	.	.	10	3	5	Moderate
Fingland Burn	5	3	7	.	.	.	.	15	10	4	Few
Mill Lade	2	1	1	3	.	.	.	7	3	4	Moderate
Westquarter Burn	6	6	4	1	.	1	.	18	10	4	Abundant
Wedderlie Burn	6	4	3	1	1	.	.	15	10	4	Moderate
Kettelshiel Burn	7	.	3	2	.	.	.	12	10	4	Few
Blackadder,											
Hallyburton	10	4	4	2	.	.	1	21	10	5	Moderate
Greenlaw	2	2	6	.	.	.	.	10	6	5	Few
Castle Mill	6	1	1	1	1	1	1	12	6	5	Abundant
Nisbet Hill	20	3	3	2	1	3	1	33	10	5	Abundant
Gordonmains,											
Greenlaw	10	2	2	.	.	.	.	14	6	5	Few
Langton Burn,											
Gavinton	12	7	1	2	.	.	.	22	10	4	Moderate
Whiteadder,											
Hungry Snout	6	2	4	2	.	.	.	14	10	4	Moderate

Table 2. Examination of stream bed for *Simulium*

Stream	No. of populated stones out of 10 examined	Maximum density per sq.in.	Remarks
Westquarter Burn	9	187	.
Water of Leith, Haugh Head	8	136	.
Blackadder, Nisbet Hill	7	240	Only at one site
Fingland Burn	4	75	150 per sq.in. in spring of 1946
Whiteadder, Hungry Snout	5	208	300 per sq.in. in August 1946
Langton Burn	5	10	Only in July and August 1947
Water of Leith, Harperrig A and B	5	3	.
Blackadder, Castle Mill	2	243	This density was only observed in July when vegetation was also densely populated. Many stones are permanently coated with moss.

A very small number of larvae and pupae was encountered very rarely on stones in the other streams.

and relative abundance of *Simulium* in the different currents and at different depths was also taken.

For measuring the current velocity of streams a waterwheel was devised. The instrument, which was found more suitable than special rheometers for use in shallow streams, consists of a circular plate of rigid,

light-weight tin with a circumference of 1 yd. Inserted on the circumference at right-angles to the plate is a series of paddle-like flanges, twelve in number and equidistant, each of which measures 2 by $\frac{3}{4}$ in., with the shorter axis in the plane of the plate. A hole in the centre of the wheel has an axle



Rippling current in Glen Beag water, 1200 ft. *Simulium variegatum* and *S. reptans*.



Cockburn, Listonshiels, 900 ft. Moderate stream, 1-2 ft. wide with dense vegetation.
Simulium latipes and *S. ornatum*.

about which the wheel can revolve freely. Smoothness of the axle and reduction of friction on it to the minimum was desirable. Satisfactory results were obtained with an axle measuring $\frac{1}{2}$ in. long and $\frac{3}{16}$ in. diameter. The axle is held in position on one side of the plate by a bolt, and on the other is attached to a metal rod which terminates in a wooden handle. On the handle side of the wheel is attached a projecting wire by which the revolutions of the wheel can be counted, either visually or by repeated contact with the hand of the operator, in a certain unit of time. The number of yards traversed by the current per 15 sec. was raised to yards per minute, and fractions were brought to the nearest whole figure. This wheel can be dismantled and packed in a box. A wheel of $1\frac{1}{2}$ ft. circumference was found not to move freely in very shallow and slow-moving water, but a wheel of 1 yd. circumference proved suitable for all speeds of current above 12 yd./min. In operation, the gauge should be vertical to the surface of the water. The flanges are the only parts which should touch the surface of the water. It was noted that under windy conditions the gauge was unreliable since they produced irregularities in rotation.

Water-levels were simply measured by a graduated scale of 3 in. units, marked on a stake of 1 yd. length. Currents were classified as belonging to three main kinds: cascades; ripples (Pl. 1); uniform. The presence of air bubbles in the water and their effect on the distribution of *Simulium* larval populations were also recorded.

Finally, attention was also given to the altitude of the streams, and the type of farming and kinds of stock present in the several areas in which the observations were made.

No claim is made to absolute accuracy in our estimates of larval population densities based on a system of random sampling. We do not pretend that the estimates have any significance apart from providing a basis for rough comparison of one larval site with another in the same or different streams; and it should be appreciated again that the variability of larval habitats and the nature of the substrata (vegetative or mineral) make the standardization of sampling for counting practically impossible. It should also be recognized that by reason of seasonal fluctuations, comparison of larval counts as between one chosen site and another can only well be drawn if they are made during one and the same season and at nearly the same time. Even then, where mixed populations of species are concerned, due allowance would require to be made for differences in seasonal development. In view of all these considerations, the data acquired and presented in the present paper must be interpreted with due caution, and can only be regarded as indicative of the relative abundance of populations.

Rearing apparatus

This consisted of a glazed earthenware tank, with inside measurements 13.5 in. wide, 22 in. long and 7 in. deep. Inside the tank is placed horizontally a U-shaped trough of glazed fire-clay, 2 in. deep, and 4 in. wide, the arms of the U being 18 in. and the cross-piece 10 in. long. A fish-tail glass jet (width 1 in. and shorter axis $\frac{1}{2}$ in.), carries a flow of water into the end of one of the arms of the U trough and maintains a current circulating round the trough. This current varies in strength in the different parts of the channel. In the first arm, the current is fastest (approximately 40 yd./min.) and water contains air bubbles, while in the cross-piece the current is moderate (approximately 20 yd./min.) with fewer air bubbles. In the other arm the current is slow (approximately 10 yd./min.) with occasional, or no, air bubbles.

In the trough along its length and under the surface of the water are arranged white tiles on which *Simulium* larvae establish themselves. After passing through the trough, the edges of which are slightly projecting above the surface of the water in the tank, the water returns to the tank. The outlet water from the tank, after passing through a strainer, is returned to an induction pump which maintains the circulation through the whole system. The outlet water from the pump is passed through a condenser to cool the water heated by the pumping action, and thence to the inlet through the fish-tail jet. Observations on the water temperature in the system are made by means of a maximum and minimum thermometer placed at the side of the tank. The bulb of this thermometer is immersed in the water of the tank and protected by a cylinder of perforated copper. The system at first was filled with stream water and tap water was added to compensate for loss by evaporation. As regards food supply, plankton from the stream was added at first, but algae and vegetable debris from plant pots were then used. A marked deficiency in the system was that food material did not permanently remain suspended in the circulating water, as most of it ultimately accumulated on the bottom of the tank. In the section below the trough, the water of which is turbulent, the larvae did not establish themselves, and those which were occasionally washed away from the trough to the bottom soon spun threads which were attached to the trough at the inlet of the circulating water. Dense colonies of larvae were observed in the moderate and slow zones when about 1500 third to final instar larvae of *S. ornatum* taken from a stream were placed in the system, which proved efficient in the rearing of penultimate instars to pupae. Success, however, was not achieved in rearing larvae from eggs to the final instar. Only ten half-grown larvae were observed up to 7 September from 2000 of first-instar larvae of *S. ornatum* placed in the system

12–18 July 1948. This high mortality is attributable to the deficiency of regular food supply, and possibly to abnormally high temperatures of 18·3–22·8° C. to which larvae were exposed for a week.

3. DISTRIBUTION OF *SIMULIUM* SPECIES IN SCOTTISH STREAMS

(a) *Habitat factors*

Scottish streams vary in their character according to the geographical areas through which they pass. In south-east Scotland they can be classified as follows:

(1) Upland, at altitudes of 700 ft. or over, traversing rough grazings occupied by Blackface sheep.

(2) Semi-upland, at altitudes of 300–700 ft., draining pastures which support Cheviots, cross-bred sheep and store cattle.

(3) Lowland, at altitudes of less than 300 ft., traversing ground that is given over to mixed farming.

The distribution of *Simulium* species depends on the different characters of streams; thus, *S. latipes* and *S. monticola* are characteristic of upland streams, *S. variegatum* and *S. reptans* of semi-upland, while *S. ornatum* is widely distributed in all three. The type of current, the nature of vegetation, the physical characters of the stream bed and the width of the stream are the important features which determine the species distribution of *Simulium*. Before discussing distribution, reference may be made to the role played by each of these factors. The detailed evidence is summarized in Tables 10 and 11.

Elevation of the stream

The important factor here is probably water temperature which varies in the several regions if measured in one day. The lowest temperatures occur in the

uplands. In the semi-uplands the temperature is usually 1–2° C. higher than in the upland districts, and the same difference may occur between the latter area and the lowland. In the descent from the upland to the lowland, the rise of temperature is not so apparent over short distances as was recorded by Stukolkina in Russia (1939), where the temperature was said to increase by about 0·5° C. for every 100 m. The following example illustrates the slight change of temperature with descent, in a Scottish stream:

The distance between two upland stations, Upper Harperrig (1100 ft.) and Lower Harperrig (900 ft.), on Water of Leith is 1·5 miles, but the change of water temperature was almost negligible.

Table 3

	Upper Harperrig (° C.)	Lower Harperrig (° C.)
25 March 1947	0·8	1·1
19 April 1947	10	10
21 August 1947	18·5	19

The species *S. ornatum*, *S. monticola* and *S. latipes* were found to breed equally in the two localities. But when the distance increased to 5 miles, there was a marked rise in the temperature of the water; correlated with this is a marked change in the species composition. At Haugh Head, 5 miles downstream from Lower Harperrig, Water of Leith, there was always a population of *S. ornatum*, *S. variegatum* and *S. reptans*. In June 1946 temperature records showed that the Haugh Head station (13·0° C.) was 1·25° C. higher than Lower Harperrig, and on 27 July 1946, the temperatures of Water of Leith at Harperrig (upland), Haugh Head (semi-upland) and Slateford (lowland) were 15·5, 16·5 and 17·5° C. respectively. In

Table 4. *Water temperatures (° C.) of Water of Leith*

Station	... Lower Harperrig B	Haugh Head	Slateford
Distance	... About 5 miles	About 12 miles	—
Altitude	... 900 ft.	600 ft.	200 ft.
Winter:			
5 Dec. 1946	2·5	3·5	4
20 Jan. 1947	1	2·5	3
Av.	1·8	3	3·5
Spring:			
16 Apr. 1947	10	12·4	13·2
17 Apr. 1947	11·75	13	14·5
29 Apr. 1947	5·5	6	6·5
Av.	9·1	10·5	11·4
Summer:			
23 July 1947	16	17	18·5
21 Aug. 1947	19	20·5	22·25
Av.	17·5	18·8	20·4
Autumn:			
19 Sept 1947	12·2	13	14
20 Oct. 1947	9·5	10	10·5
Av.	10·9	12	12·3

Table 4 the average temperature of the above three localities is given at different seasons of 1947.

On 7 March 1948, there was a considerable difference between temperatures at Lower Harperrig and Haugh Head, 4 and 8° C. respectively.

Type of current

S. monticola, *S. tuberosum* and *S. variegatum* prefer cascading and pronouncedly rippling currents, but the last was also found in moderately rippling currents, where it occurs with *S. reptans*. *S. variegatum*, unlike *S. reptans*, was not found in weak rippling waters. *S. latipes* is characteristic of very slow uniform currents. *S. ornatum*, which survives in all types of current, was apt to be absent or scanty in cascading and strong rippling currents.

Velocity and type of current

From field experience we have evolved an arbitrary system of classification of current speeds, which is detailed as follows:

- (1) Slow current less than 12–24 yd./min.
- (2) Moderate current 24–48 yd./min.
- (3) Fast current 48–96 yd./min.
- (4) Spates, current over 96 yd./min.

In their appropriate habitat, *Simulium* larvae show marked preference for certain types of currents and current velocities.

The minimum current rate for larvae differs with different species. Fairly dense colonies of *S. latipes* and *S. ornatum* were found in uniform currents (less than 12 yd./min.), whilst those of *S. monticola*, *S. variegatum* and *S. tuberosum* were scantily present in uniform currents of less than 24 yd./min., but small populations of *S. reptans* may be found in smooth currents of less than 24. Scanty populations of *S. aureum* and *S. equinum* were occasionally found in uniform currents of less than 16 yd./min. The current rate may, however, be modified by changes in the physical features of the substrata; for example, accumulation of sediment and growth of algae may alter the suitability of larval habitats (Table 5). The stony beds of slow stretches of streams, particularly those with uniform currents, are apt to become covered with sedimentary deposits and heavy overgrowths of algae, and the coated stones become unfavourable for larval occupation. Low water accompanied by a heavy growth of algae and a thick deposit of sediment on both vegetation and stones may induce larvae to migrate to cleaner sites. This was evidenced by a sudden drop in the populations present at several points in the Blackadder Water, during the warm dry summer of 1947, of which Wedderlie is given as an example in Table 5.

The maximum current rate tolerance also differs for different species of *Simulium*. At normal water-

levels densities of *S. ornatum* decrease at velocities of over 72 yd./min. where water is cascading or strongly rippling, *S. variegatum*, *S. monticola*, *S. tuberosum* and *S. reptans* at 96, and *S. aureum* and *S. equinum* at 72. This was further evidenced by the presence of larvae at greater depths during spates, and larvae were occasionally observed shortly after rainfall (which caused a slight increase in water-level of 3–4 in.) to have congregated in a sheltered site on submerged vegetation about 1–2 yd. distant from their original haunts. Larvae in water of normal level in summer are mainly found at the surface on trailing and floating vegetation. It seems probable that larvae soon after experiencing a rise in current rate, seek shelter often at depths where the velocity of the current is low. Those which do not succeed in gaining suitable shelter may be washed downstream, where their re-establishment is purely fortuitous.

It has been noted that larvae, as soon as they are detached from their substratum, spin threads, which may extend to about a yard in length. The larvae may remain attached to these threads for a considerable time, and would probably try to resume their original position, but do not always succeed in doing so, as Pomeroy (1916) remarked. Our experience shows that they either contrive to secure a stance nearby or are washed downstream should the thread break. These larvae are thus removed from primary sites where they are found on hatching, to secondary sites, which they proceed to colonize. How far detached larvae may be carried downstream has not been determined, but from circumstantial evidence the secondary sites are usually not far from the primary ones, since the larvae of hill-stream species, except *S. latipes*, were not found in lowland stretches inspected after spate conditions. In semi-upland stretches of stream larvae of hill species, such as *S. monticola*, were regularly found, although in small numbers, in collections obtained after spates. The numbers of larvae of *S. monticola*, however, were high only on one occasion in the Whiteadder at Hungry Snout, after a prolonged period of high flooding in the spring of 1947. Again *S. latipes* seems to be carried in larger numbers by spate water to semi-upland stretches as evidenced by appreciable larval populations of this species found in the latter following spate conditions. This may be attributed to the fact that *S. latipes* larvae inhabit slow-moving waters and are readily removed from their substrata with a sudden rise in the strength of the current.

To test the effect of floods on transport of larvae, a plankton net was operated for 1 hr. at high water in the Water of Leith at Haugh Head on 6 February 1948, during which time seven larvae were collected (four *S. latipes*, two *S. ornatum* and one *S. variegatum*). The results agree with those of Butcher *et al.* (1937), who reported the collection of a small number of

Table 5. Effect of sedimentary deposits and algal growth on *Simulium* populations

Station	July 1947*					August 1947*				
	Popula- tion per sq.ft. of vegeta- tion†	Current velocity (yd./ min.)	Species	Percent- age	Popula- tion per sq.in. on stones†	Popula- tion per sq.ft. of vegeta- tion	Current velocity (yd./min.)	Species	Percent- age	Popula- tion per sq.in. on stones
Water of Leith, Haugh Head										
I A	100	32-42	?	.	.	111	16-24	<i>S. reptans</i>	50	.
								<i>S. ornatum</i>	50	.
B	700	64	?	.	.	1800	36-40	<i>S. reptans</i>	34	.
								<i>S. ornatum</i>	56	.
								<i>S. variegatum</i>	10	.
C	2/10	60-84	?	.	.	3/10	40-52	<i>S. reptans</i>	69	.
								<i>S. ornatum</i>	1	.
								<i>S. variegatum</i>	30	.
II A	250	20	<i>S. reptans</i>	80	.	<i>Si. abs.</i>	12	<i>Si. abs.</i>	.	.
B	250	24	<i>S. ornatum</i>	20	.	19	12	<i>S. reptans</i>	21	.
								<i>S. ornatum</i>	79	.
C	†	.	<i>Si. abs.</i>	.	.	†	.	<i>Si. abs.</i>	.	.
III A	100	28	<i>S. reptans</i>	72	.	4	12	<i>S. ornatum</i>	100	.
B	100	32	<i>S. ornatum</i>	23	.	22	12	.	.	.
			<i>S. variegatum</i>	5	.			.	.	.
C	†	.	<i>Si. abs.</i>	.	.	†	.	<i>Si. abs.</i>	.	.
IV A	2156	64	<i>S. reptans</i>	52	.	1974	48	<i>S. reptans</i>	61	.
B	2050	56	<i>S. ornatum</i>	11	.	1462	40	<i>S. ornatum</i>	37	.
			<i>S. variegatum</i>	7	.			<i>S. variegatum</i>	2	.
			<i>S. undetermined</i> (small larvae)	30	.					.
C	8/10	40-80	<i>S. reptans</i>	77	72-90	7/10	32-52	<i>S. reptans</i>	67	88-133
			<i>S. variegatum</i>	23				<i>S. ornatum</i>	4	
								<i>S. variegatum</i>	28	
								<i>S. monticola</i>	1	
V A	710	48	<i>S. reptans</i>	61	.	932	24-36	<i>S. reptans</i>	45	.
B	817	40	<i>S. ornatum</i>	23	.	1032	28-32	<i>S. ornatum</i>	53	.
			<i>S. variegatum</i>	6	.			<i>S. variegatum</i>	2	.
			<i>S. undetermined</i>	10	.					.
C	6/10	40-80	<i>S. reptans</i>	40	120-135	6/10	36-48	<i>S. reptans</i>	72	60
			<i>S. ornatum</i>	4				<i>S. ornatum</i>	5	
			<i>S. variegatum</i>	56				<i>S. variegatum</i>	23	
Wedderlie Burn, Westruther										
I A	205	24	<i>S. ornatum</i>	94	.	.	<12	<i>Si. abs.</i>	.	.
B	139	16	<i>S. monticola</i>	4.5	.	.	<12	<i>Si. abs.</i>	.	.
			<i>S. latipes</i>	1.5	.	.				.
C	†	.	<i>Si. abs.</i>	.	.	†	.	<i>Si. abs.</i>	.	.
II A	Veg. abs.	.	<i>Si. abs.</i>	.	.	Veg. abs.	.	<i>Si. abs.</i>	.	.
B	300	24-36	<i>S. ornatum</i>	98	.	.	12-20	<i>Si. abs.</i>	.	.
			<i>S. monticola</i>	2	.					.
C	.	.	<i>Si. abs.</i>	.	.	.	.	<i>Si. abs.</i>	.	.
III A	.	16	<i>Si. abs.</i>	.	.	.	<12	<i>Si. abs.</i>	.	.
B	.	16	<i>Si. abs.</i>	.	.	.	<12	<i>Si. abs.</i>	.	.
C	†	.	<i>Si. abs.</i>	.	.	†	.	<i>Si. abs.</i>	.	.
IV A	949	40-60	<i>S. ornatum</i>	60	.	.	20-40	Egg masses of	.	.
			<i>S. monticola</i>	20	.			<i>S. ornatum</i> &		
			<i>S. undermined</i>	20	.			<i>S. aureum</i>		
B	Veg. abs.	.	<i>Si. abs.</i>	.	.	Veg. abs.	.	<i>Si. abs.</i>	.	.
C	†	.	<i>Si. abs.</i>	.	.	†	.	<i>Si. abs.</i>	.	.
V A	200	40	?	.	.	.	<i>Si. abs.</i>	<i>Si. abs.</i>	.	.
B	200	40	?	.	.	.	<i>Si. abs.</i>	<i>Si. abs.</i>	.	.
C	†	.	<i>Si. abs.</i>	.	.	†	<i>Si. abs.</i>	<i>Si. abs.</i>	.	.

* In July deposits of sediments and algae were slight but considerably increased in August. At Haugh Head these two factors affected the larval population of the slow uniform current (sites II and III), but in Wedderlie sediment and algae were abundant at all sites except site IV, which was relatively cleaner. Absence of all larval population in Wedderlie, however, is noted in August. In this month there was oviposition at site IV. This accounted for a population found in September at the same site 1011 per sq.ft. of vegetation and also 900 at site V, identified as follows: 42 % *S. aureum*, 16 % *S. ornatum*, 42 % spp. undetermined—small larvae. Other sites of Wedderlie—I, II and III—were not populated in September because of the presence of silt and algae.

† Population is given per sq.ft. of vegetation collected from edges of banks A and B and for the stream bed C (p. 35).

‡ Fixed stones, permanently coated.

Veg. abs. = vegetation absent.

? = Undetermined.

Si. abs. = *Simulium* absent.

Simulium larvae in a medium tow-net dragged at the surface of the water in the River Tees for 10 min. during a flood.

Populations of *Simulium* larvae in streams are subject to various vicissitudes, not least of which are prolonged periods of summer drought, when hill streams may partly or completely dry up and the pupae and egg masses are consequently destroyed. Under these conditions surviving larvae tend to seek any available trickle of water under the surfaces of stones.

Mode of influence of current velocity on Simulium populations

As a general rule denser congregations of *Simulium* larvae are to be found in moderate and fast than in slow currents, with the exceptions of *S. ornatum* and *S. latipes* which are found in abundance in very slow-running water where they lived permanently. (At Cockburn, Listonshiels, 1013 larvae per square foot of vegetation occurred in a current of 16–20 yd./min. on 19 July and 459 on 18 August in a current of less than 12 yd./min.).

The selection of faster currents by the larvae of most species has been considered by most workers as caused by the preference for well-aerated positions which were supposed to be produced by agitation of the water. Having analysed the dissolved oxygen contents of water samples from both fast and slow currents, we find that there is little difference in the amount of oxygen saturation relative to current speed (Table 6).

Table 6. *Oxygen saturation of slow and fast currents*

Site	Current velocity (yd./min.)	Percentage oxygen saturation at 18° C.
I	16	100.3
II	40–65	100.9

Another sample from a very slow stretch (12 yd./min.) in Wedderlie Burn, gave an oxygen saturation of 97.1 %. In short, disturbance of the water does not seem to increase the amount of dissolved oxygen. From this evidence it can be concluded that oxygen is not the determining factor for the preference of larvae for fast currents, and this confirms Wu's

findings (1931). Furthermore, abundant colonies of *S. ornatum* have been found at an oxygen saturation level of as low as 48 % at 18° C. in Westquarter Burn, Stirlingshire. Butcher *et al.* too (1937) found abundance of the same species in the polluted waters of the Skerne, along with a small population of *S. reptans* and *S. aureum* larvae. But contrary to Wu, who considered food as of secondary importance compared with the current-rate itself, we found that food is a factor of primary importance in determining larval positions, since at any given point in a fast current a larger quantity of plankton will pass in a given time than at a comparable point in a slow current in the same period of time. The following data (Table 7) were obtained by the use of a plankton net of 4.5 in. in diameter, which was held in the stream for 1 min. and dragged for 1 yd. length against the current ten times in succession. The samples were filtered and dried in an oven at 50° C.

It can be seen that the ratio of the amount of plankton in fast and slow currents was, in the Water of Leith 10:1, and in the Westquarter Burn 7.9:1.

Correlated also, as mentioned earlier, with current velocity is the factor of sedimentation. In slow currents, such as Westquarter I where sedimentary deposits are heavy, *S. ornatum* does not occur, whilst in the Mill Lade and Cockburn where less silting takes place, it was found abundantly in currents of less than 12–20 yd./min.

Simulium larvae, under natural conditions and according to our observations in the rearing apparatus, are almost entirely dependent upon their head fans for feeding, as was described by Smart (1934a). The alternative method described by the same author, of scraping vegetable debris from the substratum, was only observed under unfavourable conditions such as in stagnant water or in slow currents.

In currents of all kinds *Simulium* larvae of all species avoid sites where the water beats directly on substrata, producing a splash and air bubbles. Dense colonies were usually found at sites where a steady flow of water passes over the larvae and is not necessarily charged with air bubbles. The latter observation contradicts that of Rubzov (1940), who maintained that denser colonies occur in water highly charged with air bubbles, which are necessary for respiration.

Table 7. *Plankton weight from slow and fast currents, Water of Leith and Westquarter Burn.*

Stream	Site	Current velocity (yd./min.)	Plankton weight (g.)	<i>Simulium</i> population per one sq.ft. of vegetation	Species
Water of Leith,	I	16	0.0180	30	<i>S. ornatum</i> and <i>S. latipes</i>
Lower Harperrig	II	40–56	0.1800	280	<i>S. ornatum</i> and <i>S. monticola</i>
Westquarter	I	< 12	0.0177	.	.
	II	36–40	0.1396	500	<i>S. ornatum</i>

Our experience, with *S. latipes* and *S. ornatum* at least, shows that they do survive in slow-moving waters devoid of air bubbles (p. 41). The example shown in Table 8 is also given as illustration of our findings on *S. monticola*, though the number of larvae was generally small.

Ten stones (surface area *c.* 6–15 sq.in.) were examined at random in an area of 2 sq.yd. of the stream bed.

and may become luxuriant in lowland streams. Poverty of vegetation in upland streams is in part attributable to severity of climate (higher rainfall and lower temperature), poor soil and periodic destruction of the bank by spates. In lowland stretches, on the other hand, presence of vegetation in its greater profuseness may be correlated with a higher state of fertility of the banks composed of richer alluvial soil. These are, in our experience, the chief factors

Table 8. *Examination of stream bed for S. monticola larvae in Harperrig B, Water of Leith*

Stone	No. of larvae per stone	Water-level (in.)	Current velocity (yd./min.)	Air bubbles
1	.	6	28	Frequent
2	.	6	28	Frequent
3	.	6	28	Frequent
4	.	7	44	Abundant
5	.	7	44	Abundant
6	1	4.5	48	Few
7	10	4.5	48	Few
8	2	4.5	48	Few
9	16	8	56	Absent
10	20	8	56	Absent

Previous authors have placed great emphasis on the oxygen requirements of *Simulium* larvae after having observed their death in still water under laboratory conditions. In this connexion we may refer to Pomeroy (1916) who stated that larvae in still water placed in a corked bottle and kept at 0° C. live longer than at 23.8° C., while in running water they live equally at both temperatures. In our opinion, mortality of larvae in still water is due to three main factors: first, that oxygen saturation in the immediate vicinity of the larvae is soon exhausted; secondly, unavailability of plankton food which drops to the bottom of the container where it is out of reach; and thirdly, accumulation of metabolic larval waste products which undergo decomposition and thus cause a further reduction of oxygen. Under natural conditions, i.e. in running water, the oxygen supply is constantly renewed, as indicated by Smart (1934*a*), food is continuously presented to the larvae and toxic metabolic wastes are regularly removed.

It should be noted here that 'a primary *Simulium* site' is that which is chosen by gravid females for the deposition of their eggs, and consequently the establishment of initial larval colonies. These sites are to be found in the proximity to faster currents. From the primary site the larvae may distribute themselves either voluntarily or as a reaction to disturbing factors, to a secondary site, which may be one that is unsuitable for egg-laying.

Vegetation

The vegetation of upland streams is very limited, but gradually increases under semi-upland conditions

determining the relative abundance of bank vegetation, whilst increases of lime, organic matter and silt (derived from sewage pollution), as assumed by Butcher *et al.* (1937) on the River Tees, may be of secondary importance.

As shown in Table 9 dense growth of vegetation occurs at North Esk, Carllops, Linhouse Water, Burnbank and Water of Leith, Haugh Head, in which streams the water is clean and relatively deficient in lime (2.65–4.55). In the upper reaches of these streams, only few species of flowering plants (mainly *Juncus*) occur in scattered patches. This vegetation deficiency is attributable to bad climate and destruction of banks by spates. The paucity of bryophytes on upland stream beds may be attributed to destruction by floods as Butcher *et al.* suggest, but according to our observations conditions of desiccation, in which many stones are left high and dry, may also have a restrictive effect.

Vegetation is an important factor in the habitat of *Simulium* since it provides a suitable support for the larvae and pupae as well as for ovipositing females. As regards preferred vegetation, our observations agree with those of Edwards (1920) who found that plants with long narrow leaves with a smooth surface are invariably preferred, as, for example, *Carex*, *Phalaris*, *Iris*, *Sparganium minimum*, *Mimulus*, *Nasturtium officinale*, *Rumex*, *Myosotis*, *Festuca elatior*, *Poa*, *Sagittaria sagittifolia*, *Holcus lanatus*, *Deschampsia caespitosa*, *Phleum*, *Nardus stricta*, *Agrostis* and *Glyceria fluitans*. The last three were often scantily populated, especially when more favoured plants such as the first five were present. Contrary to

Table 9. *Density of vegetation related to local land conditions and increase of temporary hardness and organic matter*

Stream	Elevation (ft.)	Land utilization	Vegeta- tion*	No. of species of flowering plants	Temporary hardness (parts per 100,000)	Nitrogen (parts per 100,000) as			Dissolved oxygen (percentage of saturation at 18° C.)
						Free and saline ammonia	Nitrites	Nitrates	
North Esk, Pentlands	1100	Rough grazing	Patchy	1	3.26	0.0090	.	.	98.6
Carlops	800	Pasture	Uniform	12	4.55	0.0040	.	.	97.9
Crosswood, Lanark Rd	900	Rough grazing	Patchy	2	2.41	0.0190	.	.	93.1
Linhouse, Burnbank	600	Pasture	Uniform	10	2.65	0.0080	.	.	93.1
Water of Leith, Lower Harperrig	900	Rough grazing	Patchy	3	3.82	0.0064	.	.	96.8
Haugh Head	600	Pasture	Uniform	6	3.38	0.0061	.	.	96.7

* Patchy vegetation = in a stretch of about 200 yards, only few scattered patches of vegetation occur, each patch about $\frac{1}{2}$ -2 yd. long. Uniform vegetation = in a stretch of about 200 yd., about two-thirds of the length of each bank is densely coated with flowering vegetation.

Rubzov (1940), we found that alder (*Alnus*) and willow (*Salix*) were also favoured by larvae of *Simulium*. Fallen pine needles and other fallen leaves in streams were also occupied by large numbers of larvae. *Mentha aquatica* was occasionally inhabited, but only by small numbers of larvae or pupae, especially when no other plants were available. Nettles (*Urtica*) and bracken (*Pteridium aquilinum*) were completely neglected and so likewise were flowers of *Juncus* spp.

The maximum density of the larval-pupal population on *Juncus* may amount to 140 larvae and pupae per 1 in. length of leaf (= 125 per sq.in.) and the average maximum count obtained from 1 sq.ft. of vegetation was 2000-3000. An exceptional record of 5168 larvae and pupae (mainly *Simulium ornatum* with very few *S. equinum*) was obtained from 1 sq.ft. of *Phalaris* leaves in Blackadder Water, Castle Mill, on 1 July 1947.

Characters of stream bed

Mosses and algae are relatively rare in upland streams, but in semi-upland streams surfaces of stones, coated with algae and sediment, are unsuitable 'footholds' for the larvae. Populations of saxicolous larvae become very scanty under such conditions, particularly if the stream is deficient in other suitable substrata such as vegetation. The following kinds of algae were found on a single stone in the Fingland Burn, Traquair, where a small population was present: *Stipitococcus*, *Spirogyra*, *Lemanea mamilliosa*, *Batrachospermum*, *B. moniliforme* (a trace), *Oedogonium*, desmids and diatoms including *Gomphonema geminatum*. Other algae which produce unfavourable

conditions of the larval substrata are *Microspora* and *Ulothrix*.

Other aquatic vegetation growing in stream beds, including *Ranunculus*, *Myriophyllum* and *Ceratophyllum*, were found to provide the larvae with a favourable substratum.

Fontinalis, *Rhacomitrium heterostichum* and *Cladophora glomerata* were occasionally colonized by a small number of larvae but were not all attractive when occurring in slow-running water.

The maximum density of a saxicolous *Simulium* population may be as much as from 250 to 350 larvae and pupae per square inch of substratum, the higher density being for larvae of a small-sized species (*S. reptans*) and the lower for larger species (*S. variegatum*, *S. monticola* and *S. ornatum*).

Plankton

Examination of the gut contents of larvae collected from various streams in different localities showed that there is a seasonal variation in the larval diet. Diatoms become predominant in the spring and at high water-levels. Algae and small insects, such as mayfly first-stage nymphs, are characteristic of the summer diet, whilst plant tissue and plant debris are common components of the winter diet. The amount of algae and diatoms increases with rainfall. It should be noted that in the summer of 1946 a wide range of variation in the size of pupae was noted and this may have been correlated with frequent rainfalls during the season. These appeared to increase the plankton and thus provided more food for larvae, which grew to a larger size in consequence. For example, cocoons of pupae of *S. ornatum* taken from Linhouse Water in

July and August 1946 measured 3.2–5 mm. (4.5–5 mm. was most prevalent) and from North Esk River, cocoons of *S. variegatum* measured 4.9–6.2 mm. (5–6 mm. prevalent).

In the summer of 1947, characterized by long, dry periods, there was an appreciable decline in the diatom plankton which was reflected in the lesser size of the maturing larvae and pupae. For example cocoons of pupae of *S. ornatum* taken from Water of Leith, Haugh Head, in July and August 1947 measured 3–4 mm. (with a few 2.8 mm.), and in September 2.5–3 mm. Also cocoons of *S. variegatum* taken from the same stream in July and August 1947, measured 3–4 mm. (with a few 6 mm.), and in September 3 mm.

Pupae of the spring generation are usually the largest; their cocoons measured as follows: *S. ornatum* 5.5–6 mm.; *S. variegatum*, 6.5–7 mm.

The amount of plankton available to an organism feeding by means of a straining mechanism (head-fans) is obviously greater when the organism is in water of a high velocity than in water of a lower velocity. Furthermore, in water of low velocity there is a loss of plankton contents due to sinking and settling of the plankton (p. 41). Ditches and small hill streams chiefly contain plant debris as identified in the gut of larvae of *S. latipes* which breed there.

Width of streams in relation to Simulium species

From the point of view of their width, streams may be divided as follows:

- (1) Rills and ditches of a temporary nature, up to 1 ft. wide, where *S. latipes* breeds.
- (2) Small streams of 1–5 ft., where *S. latipes* and *S. ornatum* breed and occasionally *S. monticola*.
- (3) Medium-sized streams of 5–10 ft., inhabited by *S. variegatum*, *S. monticola* and *S. tuberosum*.
- (4) Wide streams of 10–20 ft., inhabited by *S. variegatum*, *S. reptans* and often *S. ornatum*.
- (5) Rivers over 20 ft., where *S. ornatum* occurs.

S. aureum was recorded once in a small stream and was occasionally found in medium-sized streams along with *S. equinum*; both species were abundantly present in wide streams and rivers.

Generally speaking, upland streams are feeders of lowland streams and rivers, and in tracing any particular stream from its source at higher elevations it becomes gradually enlarged in its descent to the semi-uplands, and lowlands and by the reception of tributaries may expand to the dimensions of a river.

(b) *Species composition of the different waters*

Rills and ditches (Table 10, no. 21; Table 11, nos. 84, 110, 117).

These seem to constitute the normal habitat of *S. latipes*, especially those of very slow current, 12–32 yd./min. at normal level. These small streams

may dry up during part of the summer, and the larvae are then forced to immigrate to the lower reaches of larger streams, where conditions are more favourable. Under spate conditions, too, numbers of the larvae are transported downstream and so distributed farther afield. Certain of these small streams in the Scottish Highlands, about 1 ft. wide, with stony beds and strong cascading and rippling currents, were found to be populated by only an occasional larva of *S. monticola*.

Small streams (Table 10, nos. 2, 16, 87; Table 11, nos. 24, 26, 30, 33, 71, 72, 104, 108, 123, 125).

These are of two classes, namely, swift and slow running. The former usually have stony beds and are clothed with sparse vegetation, cascades alternating with short quiet stretches. Here *S. monticola* is common and may be associated in summer with small numbers of *S. latipes* (streams nos. 26, 33, 87.) In slow-running streams *S. latipes* becomes predominant, and where the streams are clad by a dense growth of vegetation on the banks or on the muddy and gravelly bottom (Pl. 2) *S. ornatum* appears together with *S. latipes* (streams nos. 2, 16). During the dry season the flow of water on these streams may be reduced to a trickle, and *Simulium* larvae are then found on the under-surfaces of stones or vegetation. The small, swift upland streams of Perthshire with stony beds were said by Smart (1936) to be populated by *S. monticola* and *S. hirtipes* Fries. Our observations agree with those of Smart in regard to *S. monticola* but *S. hirtipes* was not encountered.* In slow, small streams Smart likewise found *S. latipes* associated with *S. ornatum*. Small streams with moderate current and patchy vegetation are often populated with *S. monticola*, *S. ornatum*, and *S. latipes* (streams nos. 24, 30, 71, 72, 104).

Medium streams: (Table 10, nos. 11, 29, 31, 63, 86; Table 11, nos. 35, 43, 51, 55, 61, 82).

In parts of such streams at elevations of about 1000 ft., characterized by cascading rippling currents alternating with small pools, *S. monticola* is the only species of *Simulium* that occurs (stream no. 55). Where the current is slow *S. latipes* appears, whereas *S. ornatum* is associated with those parts that are fringed with aquatic plants but does not usually occur on the leaves of the few plants that grow close to

* While the author was visiting the Freshwater Biological Association at Wray Castle, Ambleside, Westmorland, England, in January 1949, he made some collections of *Simulium* larvae. It was surprising that *S. hirtipes* occurred along with *S. monticola* in small and medium swiftly running streams of an upland area. This seems to be the first record of *S. hirtipes* for England. Rills and ditches of that area were occupied by *S. latipes*.

Table 10. *Distribution of Simulium species in Scottish streams (regular observations 1946 to 1948)*

(1 = Most predominant; 2 = second most predominant; 3 = third most predominant; * = Occasional in small numbers; † = Occasional in large numbers.)

Stream and locality	No.	Eleva- tion (ft.)	Stream width (ft.)	Predominant current			Simulium species							Notes			
				Cascades	Ripples	Uniform, fast	Uniform, slow	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. variegatum</i>	<i>S. reptans</i>	<i>S. latipes</i>	<i>S. tuberosum</i>		<i>S. aureum</i>	<i>S. equinum</i>	<i>S. venustum</i>
Crosswood Burn	1	900	7-9		+	+	+	1	*	-	-	-	-	-	-	-	-
Black Burn	2	800	3-4					1	-	-	-	-	-	-	-	-	-
Linthouse Water	3	700	12-15		+	+	+	1	-	3	2	3	-	-	-	-	-
Linthouse Water, Burnbank	4	600	15-21		+	+	+	1	-	3	2	-	-	-	-	-	-
Linthouse Water, near Midcalder	5	400	15-21		+	+	+	1	*	3	2	-	-	-	-	-	-
Linthouse Water, Midcalder	6	300	15-21		+	+	+	1	-	3	3	-	-	-	-	-	-
Murrieston Water, Nether Williamstan	7	500	10-14		+	+	+	1	-	2	3	-	-	-	-	-	-
Murrieston Water, Midcalder	8	300	15-21		+	+	+	2	-	1	3	-	-	-	-	-	-
River Almond	9	130	20-24		+	+	+	1	-	-	-	-	-	-	-	-	-
North Esk, Pentlands	29	1100	6-9		+	+	+	3	1	3	-	-	-	-	-	-	-
North Esk, Carllops	31	800	6-10		+	+	+	3	2	1	-	-	-	-	-	-	-
North Esk, Penicuik	32	600	15-18		+	+	+	3	-	1	-	-	-	-	-	-	-
North Esk	33-40	400-25	20-60		+	+	+	-	-	-	-	-	-	-	-	-	-
Water of Leith, Upper Harperrig	11	1100	6-9		+	+	+	2	1	-	-	-	-	-	-	-	-
Water of Leith, Lower Harperrig	12	900	7-10		+	+	+	2	1	-	-	-	-	-	-	-	-
Water of Leith	14	800	12-15		+	+	+	1	-	3	2	3	-	-	*	-	-
Water of Leith, Haugh Head	15	650	15-18		+	+	+	1	*	3	2	-	-	-	-	-	-
Water of Leith, Whelpside	17	600	15-18		+	+	+	1	*	3	2	-	-	-	-	-	-
Water of Leith, Balerno	18	550	30		-	+	+	1	-	-	-	-	-	-	-	-	-
Water of Leith, Slateford	19	200	30		+	+	+	1	-	-	-	-	-	-	-	-	-
Cockburn	16	900	1-2		+	+	+	2	-	-	-	-	-	-	-	-	-
Ditches, Pentlands	21	1000	1		+	+	+	-	-	-	-	-	-	-	-	-	-
Small stream, Pentlands	22	900	1-3		+	+	+	2	1	-	-	-	-	-	-	-	-
Fingland Burn	63	600	8-10		+	+	+	*	1	2	-	-	-	-	-	-	-
Mill Lade	64	600	1-2		+	+	+	1	-	-	-	-	-	-	-	-	-
Quair Water	62	700	12-15		+	+	+	1	-	2	1	-	-	-	-	-	-
Wedderlie Burn	70	700	5-10		+	+	+	1	-	2	-	-	-	-	-	-	-
Kettleshiel Burn	73	700	4-5		+	+	+	1	-	-	-	-	-	-	-	-	-
Blackadder Water, Hallyburton	74	600	8-12		+	+	+	1	-	-	-	-	-	-	-	-	-
Blackadder Water, Greenlawdean	75	500	12-15		+	+	+	1	-	3	-	-	-	-	-	-	-
Blackadder Water, Greenlaw	76	500	12-15		+	+	+	1	-	-	-	-	-	-	-	-	-
Gordonmains Burn	77	500	3-4		+	+	+	1	-	-	-	-	-	-	-	-	-
Blackadder Water, Castle Mill	78	500	15-18		+	+	+	1	-	-	-	-	-	-	-	-	-
Blackadder Water, Nisbet Hill	80	300	15-21		+	+	+	1	-	-	-	-	-	-	-	-	-
Blackadder Water, Kelloe House	81	250	45		+	+	+	1	-	-	-	-	-	-	-	-	-
Langton Burn, Gavinton	83	400	6-10		+	+	+	1	-	-	-	-	-	-	-	-	-
Whiteadder Water, Kingside	86	900	9-12		+	+	+	1	2	3	-	-	-	-	-	-	-
Whiteadder Water, Hungry Snout	88	800	24-32		+	+	+	3	1	2	1	-	-	-	-	-	-
Tributary at Hungry Snout	87	800	1-3		+	+	+	-	-	-	-	-	-	-	-	-	-
Whiteadder Water, Ellemford	89	600	45		+	+	+	3	1	2	1	-	-	-	-	-	-
Whiteadder Water, Cockburn Mill	90	350	45		+	+	+	-	-	1	2	-	-	-	-	-	-
Whiteadder Water, Blanerne	91	200	45		+	+	+	-	-	-	-	-	-	-	-	-	-
Westquarter Burn	92	100	12-15		+	+	+	1	-	-	-	-	-	-	-	3	-

Notes. (1) In wooded streams *Simulium* populations were generally absent, but in Linthouse Water a very small number of larvae and pupae was occasionally found on fallen leaves and a few stones. (2) The North Esk below Penicuik is heavily polluted with chemicals discharged from paper mills, but in Water of Leith, Balerno, the discharge from a smaller number of paper mills is diluted, and a small population of *S. ornatum* was always present.

Table 11. *Distribution of Simulium species in Scottish streams (occasional observations 1945 to 1948)*

Stream	No.	Elevation (ft.)	Stream width (ft.)	Predominant current				General density	Simulium species					Other species present	
				Cascades	Ripples	Uniform fast	Uniform slow		<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. variegatum</i>	<i>S. reptans</i>	<i>S. latipes</i>		
(+ = present; (+) = very small numbers; - = absent.)															
Lothians:															
Gogar Burn	10	150	6-8	-	+	-	-	Ab.	+	-	-	-	-	-	.
Sinkle Syke	13	900	3	-	+	-	+	Few	-	-	-	-	(+)	+	.
Bonaly Burn	23	1000	3	-	-	-	-	Ab.	-	-	-	-	-	-	.
Bonaly Burn	24	500	3-5	-	+	-	-	Few	(+)	-	-	-	+	+	.
Bonaly Burn	25	200	3-6	-	+	-	-	Few	-	-	-	-	+	+	.
Braid Burn	26	800	2-3	-	+	-	-	Ab.	+	-	-	-	+	+	.
Burdiehouse Burn	27	350	3-5	-	+	-	-	Ab.	+	-	-	-	+	+	.
Figgate Burn	28	50	3-5	-	+	-	-	Few	+	-	-	-	+	+	.
Fairliehope Burn	30	1100	1-2	-	+	-	+	Few	-	-	-	-	+	+	.
Kirk Burn	33	1000	1-2	-	+	-	-	Few	+	-	-	-	(+)	+	.
Glencorse Burn	34	700	3-6	-	+	-	-	Few	+	-	-	-	-	-	.
Glencorse Burn	35	600	9-12	-	+	-	-	Few	+	-	(+)	-	-	-	.
Park Burn	38	400	3-4	-	+	-	+	Few	+	-	-	-	+	+	.
Gladhouse Reservoir	41	1000	1-2	-	+	-	+	Few	+	-	-	-	+	+	.
Fullarton Burn	43	900	5-10	-	+	-	-	Few	(+)	(+)	-	-	-	-	.
Kell Burn	85	1000	3-4	-	+	-	-	Mod.	(+)	-	-	-	-	-	.
Gifford Water	46	200	18	-	-	-	+	Few	(+)	-	-	-	-	-	A few <i>S. equinum</i>
River Tyne	47	200	12-15	-	+	-	-	Ab.	+	-	-	-	-	-	.
River Tyne	48	200	9-12	-	+	-	-	Mod.	+	-	-	-	-	-	.
River Tyne	49	200	8-10	-	+	-	+	Few	+	-	-	-	-	-	.
Arnet Water	50	1000	2-3	-	-	-	+	Few	+	-	(+)	-	-	-	.
Arnet Water	51	800	9-12	-	+	-	+	Ab.	(+)	+	-	-	-	-	.
Gala Water	52	900	3	-	+	-	-	Few	-	(+)	+	-	-	-	.
Gala Water	53	700	15-17	-	+	-	-	Ab.	-	-	-	-	-	-	.
Heriot Water	54	800	15	-	+	-	-	Mod.	-	-	-	-	-	-	.
Lady-side Burn	55	1000	5-7	+	+	-	-	Ab.	-	+	(+)	-	-	-	.
Dewar Burn	56	1100	3-5	+	+	-	-	Mod.	-	-	(+)	-	-	-	.
Peeblesshire:															
Glentress Water	57	1000	6-8	-	+	-	-	Few	-	+	(+)	-	+	+	.
Eddleston Water	58	600	9	-	+	-	-	Mod.	+	+	-	(+)	+	+	<i>S. aureum</i> , 1 %
Meldoun Burn	59	900	4-6	+	+	-	-	Mod.	(+)	+	+	-	-	-	.
Baddingsill Burn	60	1000	7-10	+	+	-	-	Mod.	-	+	+	-	-	-	.
Powsil Burn	61	700	6-9	+	+	-	-	Mod.	-	-	+	-	-	-	.
Selkirkshire:															
Yarrow Water	65	700	30-45	-	+	-	-	Ab.	-	-	+	+	-	-	.
Berwickshire:															
Leader Water	66	700	9-12	-	+	-	-	Ab.	+	-	(+)	+	-	-	A few <i>S. equinum</i>
Leader Water	67	600	24-30	-	+	-	-	Few	+	-	-	+	-	-	<i>S. aureum</i>
Boondreich Water	68	300	15-18	-	+	-	-	Mod.	+	-	-	-	-	-	.
Eden Burn	69	600	3	-	+	-	-	Few	+	-	-	-	+	+	.
Millknowe Burn	71	700	2-3	-	+	-	-	Few	+	(+)	-	-	+	+	.
Bogpark Burn	72	700	3	-	+	-	-	Few	+	(+)	-	-	+	+	<i>S. venustum</i> , <i>S. equinum</i>
Blackadder	79	500	21-24	-	+	-	-	Few	(+)	+	(+)	-	-	-	May 1947
Lint Mill	82	500	6-7	-	+	-	+	Few	+	+	-	-	+	+	.
Kirk Burn	83	1000	1-1	-	+	-	+	Few	+	+	-	-	-	-	.
Hardens Hill	84	1000	1-1	-	+	-	+	Few	+	+	-	-	+	+	.

strong cascades. All these species may be found together in parts of streams where cascades and rippling currents are of moderate pace (streams nos. 11, 43, 82). In lower reaches at elevations of about 600–700 ft., *S. variegatum* and *S. tuberosum*, associated with *S. monticola*, are to be found in sections of the stream where the rate of the current may be anything from 20 to 96 yd./min. ($\frac{3}{4}$ –3 miles/hr.) (stream no. 63).

Wide streams: (Table 10, nos. 4, 5, 7, 8, 14, 15, 17, 62, 88; Table 11, nos. 53, 65, 67).

In wide streams of upland and semi-upland regions, there are found *S. tuberosum*, *S. reptans* and *S. variegatum* (stream no. 62). *S. ornatum* may also occur where vegetation and a moderate current (not torrential) is present. The reduction of cascades, moderately rippling currents and increase of vegetation are characteristic of the wider streams in the semi-upland, and here *S. reptans*, *S. variegatum* and *S. ornatum* are found in abundance (streams nos. 4, 5, 6, 7, 8, 14, 15, 17, 88). The velocity of such streams in the lower parts of the upland is about 20–96 yd./min. and at lower levels in the semi-upland is reduced to 12–84 yd./min., where longer stretches of slow smooth current becomes more frequent.

Lowland streams: (Table 10, nos. 9, 19, 81, 91, 92; Table 11, nos. 25, 28, 46, 47, 48, 49, 94, 97, 98, 100, 101).

All kinds of small, medium, wide and river types may be present in the lowland, but the last two are of most common occurrence. As a general rule *S. ornatum* was found in all, often alone, but in the larger streams and rivers, in particular near the border of the semi-upland where current is smoother, *S. reptans* and sometimes *S. variegatum* may occur along with *S. ornatum* (streams nos. 6, 8, 89). The last eventually becomes predominant in the lowland proper. Larvae of *S. ornatum* do not seem to be wholly identified with vegetation in lowland streams, for it was found in abundance in streams with but sparse vegetation (Table 2, Westquarter Burn).

Wooded streams

Contrary to the opinion of Edwards (1920) who recorded *S. reptans* as occurring in wooded streams, our experience has been that *Simulium* larvae are absent from streams closely overhung by the foliage of trees (Table 10, nos. 5, 32). Similarly, Smart (1936) commented upon the absence of *S. hirtipes* in closely wooded streams in Fortingal, Perthshire. However, in open stretches of otherwise wooded streams large larval populations may occur (Table 10, nos. 6, 8).

(c) Notes on species and their association

(1) *Simulium ornatum*

This species is widely distributed in upland, semi-upland and lowland areas. Often it is the only black-fly of lowland streams, where it occurs in very large numbers, and this may have led Smart (1944) to assume that it is a lowland species. Actually it occurs in reaches of streams of moderate current at both high and low elevations (Tables 10 and 11) provided they support plants with leaves trailing in the water, a feature previously remarked by Edwards (1920), Pentelov (1935) and Smart (1944). It is not found in rapid hill streams, especially in the absence of vegetation. That the vegetation factor is all important in the distribution of *S. ornatum* was markedly evident in two streams at Traquair, Peeblesshire. One of these, the Fingland Burn (Pl. 2, photo 3; Table 12), poor in vegetation and with a fast torrential current, had *S. monticola*, *S. variegatum* and *S. tuberosum*, but *S. ornatum* was not represented. In the other (Pl. 3), the Mill Lade, a short channel rich in vegetation, of slow even flow, which derives from the Fingland Burn and flows into a nearby mill pond, *S. ornatum* was abundant (Table 13). (*S. ornatum* appeared scantily in the Fingland after its confluence with the run-off from the mill pond.) This stream preference of *S. ornatum* is explained by the fact that the females normally choose the leaves of plants trailing in the water to lay their eggs (Fig 1 (1)). Even on such small patches of vegetation as did occur in the Fingland and a hill stream of similar type, the Powsil Burn, Drummelzier (Table 11, no. 61), the eggs of *S. ornatum* were never found. In both of these streams the faster currents contrasted markedly with the more sluggish one of the Mill Lade and possibly did not offer the necessary security of stance for egg-laying females. There is also the added consideration that summer droughts adversely affect the Fingland and make it less attractive to ovipositing females.

In lowland streams, the larvae of *S. ornatum* are usually found on the leaves of aquatic plants and also on stones. On the latter they may occur in large colonies in parts where vegetation is sparse. Thus they have been found attached to stones in the bed of the River Tyne near its confluence with the Gifford Water (Table 11, no. 46), and again in the Westquarter Burn Lauriston (Table 10, no. 92; Pl. 4), in both of which vegetation at the place examined is scanty. But, of course, larvae may become detached from their primary sites on leaves and carried downstream with the current to secondary sites on water-washed stones.

In their survey of the River Tees, Butcher *et al.* (1937) attributed the absence of *S. ornatum* in the lower reaches—where it is replaced by *S. equinum* and *S. reptans* var. *galeratum*—to the lesser hardness of the



Mill Lade, Fingland Burn, 600 ft. Slow current, channel 1-2 ft. wide, rich vegetation. *Simulium ornatum*, *S. monticola*, *S. variegatum*, *S. latipes*, *S. tuberosum* and *S. aureum*.



Westquarter Burn, Lauriston, 100 ft. Rather fast lowland stream, 12-15 ft. wide, with scanty water plants. *Simulium ornatum* larvae were here attached to stones, where vegetation was sparse.

Table 12. *Percentage species composition of Fingland Burn, Traquair, summer 1947**

Date	<i>S. monticola</i>	<i>S. variegatum</i>	<i>S. tuberosum</i>	<i>S. reptans</i>	Total no. in all samples
May	47	3	50	.	326
June	Mass emergence ? 100		Occ. pupae and many cocoons	.	1860
Aug.	87	12	.	1	1321
Sept.	Silt, algae, decaying vegetation, slow water conditions ? Undetermined owing to absence of pupae			.	2

* Percentages in Tables 12-26 were obtained by identifying representative samples taken from samples collected.

Table 13. *Percentage species composition of Mill Lade, Traquair, summer 1947*

Date	<i>S. ornatum</i>	<i>S. variegatum</i>	<i>S. monticola</i>	<i>S. latipes</i>	<i>S. tuberosum</i>	<i>S. aureum</i>	<i>Simulium</i> undet.*	Total no. in all samples
May*	Occ.	2	32	Occ.	66	.	.	211
June†	.	.	.	.	.	.	.	.
Aug.	79.0	.	.	14.5	.	1.5	5	1432
Sept.	100	.	.	Occ.	.	.	.	.

* Stones 4/10 (12-15 per sq.in.)

† Vegetation cleared out.

Table 14. *Percentage species composition of Cockburn, Listonshiels, summer 1947*

Date	<i>S. ornatum</i>	<i>S. latipes</i>	<i>Simulium</i> undet.*	Total no. in all samples
May	44	56	.	120
June	.	5	95	500
July	12	12	76	2013
Aug.	47	48	5	918
Sept.	99	1	.	290

* Sp. undetermined = very small larvae (1st, 2nd and 3rd instars)

water and lesser sewage pollution than occurs in the River Skerne and its tributary, where *S. ornatum* is abundant. As it has been our experience that *S. ornatum* occurs in all kinds of water, hard or soft, clean or polluted (Table 8), some other reason for its absence in the Tees must be sought. The chances are that it would at least occur in the upper reaches and feeders of the river.

As investigation of the breeding conditions of *Simulium* proceeded it became apparent that, whilst colonies of single species of larvae might be found in pure culture under particular environmental conditions, it was not uncommon to find that colonies were composed of two or more species. To illustrate this admixture it will be sufficient to state our experience with *S. ornatum*, which is widespread in both lowland and hill streams. Often it occurs by itself, especially in lowland streams, whilst in small upland streams of slow or moderate current it is frequently accompanied by *S. latipes* (Table 14) and in semi-upland streams by *S. monticola*. In the latter case the numbers of *S. ornatum* varied indirectly with the strength of current and the number of interspersed cascades. Sometimes all three species occurred as

components of single colonies in upland and semi-upland streams (Tables 15 and 16), but the comparative paucity of larvae of *S. latipes* suggested that it was an unusual intruder, which had been transported by flood waters from its more customary sites in reaches farther upstream or derived from eggs laid by females when their usual habitats had dried up. Other species that were found in *S. ornatum* colonies in hill streams were *S. variegatum* and *S. tuberosum*, which were also recorded along with *S. monticola* and *S. ornatum* in the North Esk on the Pentlands, Whiteadder, Kingside and in the Mill Lade at Traquair, but only after spring spates (Table 13, May 1947). On other occasions *S. reptans* (Table 17) was often linked with *S. ornatum* and *S. variegatum* in semi-upland streams and the upper reaches of lowland streams (Table 10, nos. 3, 4, 6, 7, 8, 14, 15, 17, 88, 89). In the latter, in Berwickshire, *S. equinum* and *S. aureum* frequently shared sites with *S. ornatum* in water characterized by a rich growth of aquatic flora and moderate steady and rippling currents (Table 10, no. 80). Finally, in the autumn of 1946, *S. venustum* was taken in colonies of *S. ornatum* in a small hill stream, the Dinnet Water, Aberdeenshire

Table 15. *Percentage species composition of Water of Leith, Upper Harperrig, summer 1947*

Date	<i>S. monticola</i>	<i>S. ornatum</i>	<i>S. latipes</i>	Total no. in all samples
May	93	.	7	53
June	83	12	5	1487
Aug.	79	5	16	430

Table 16. *Percentage species composition of Water of Leith, Lower Harperrig, summer 1947*

Date	<i>S. monticola</i>	<i>S. ornatum</i>	<i>S. latipes</i>	<i>S. tuberosum</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	87	.	13	.	.	.	140
June	.	6	9	67 pupae and cocoons	.	18	34
July	20	52	1	.	.	27	478
Aug.	3	96	1	.	.	.	388
Sept.	95	.	.	.	5	.	93

Table 17. *Percentage species composition of Water of Leith, Haugh Head, summer 1947*

Date	<i>S. ornatum</i>	<i>S. variegatum</i>	<i>S. reptans</i>	<i>Simulium</i> undet.	Total no. in all samples
May	10	17	73	.	922
June	20	1	21	58	1656
July	15	16	63	6	7233
Aug.	43	10	47	.	7356
Sept.	80	19	1	.	2692

Table 18. *Percentage species composition of Whiteadder Water, Hungry Snout, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. variegatum</i>	<i>S. reptans</i>	<i>S. latipes</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	2	58	22	18	.	.	.	356
June	10	12	.	1	1	.	76	1595
1 Aug.	3	.	14	82	.	1	.	493
28 Aug.	9	.	4	20	13	5	49	223

(Table 11, no. 131) (and again in the spring of 1947), and there was a single record of an association of *S. nollerii* and *S. ornatum* in a lowland stream, Schochie Burn, Perthshire (Table 11, no. 100).

(2) *Simulium monticola*

In comparison with *S. ornatum*, *S. monticola* which is of a more restricted distribution may be cited. This species, like *S. hirtipes*, is normally an inhabitant of rapid mountain streams at elevations of 500 to 1000 ft. where the larvae, as previously remarked by Smart (1936), occupy the surfaces of stones immersed in the very rapid parts of cascades. *S. monticola* is not necessarily identified with the presence of aquatic vegetation. As already noted, it may occur with *S. latipes* and *S. ornatum* under certain conditions and has been recovered in larger semi-upland streams along with *S. variegatum* alone (Table 11, no. 61) or combined with *S. tuberosum* (Table 10, no. 63). Whilst *S. monticola* is not a usual inhabitant of wide streams and rivers, it has been collected by Butcher *et al.* (1937) in the Tees with *S. variegatum* and again

by ourselves in the Whiteadder, Berwickshire. It appeared in the latter in appreciable numbers in May 1947 (Table 18) after prolonged spates which involved both the river and its tributaries. Evidently it had been borne there in flood waters from the upper reaches of the hill streams. Its egg mass is illustrated in Fig. 1 (5).

(3) *Simulium variegatum*

This species has not been observed under natural conditions in pure culture. As has already been stated, it was found in association with *S. monticola* and *S. tuberosum* in the strong rapids of semi-upland streams, its primary habitat. From there it may wander downstream to secondary sites, where it occurs with *S. reptans* and sometimes *S. ornatum* in larger streams and rivers, in which the current is less torrential and smoother. Edwards's opinion (1920) that the species replaces *S. ornatum* in hill streams is, in our experience, true only when medium-sized hill-streams have poor vegetation, e.g. the Fingland and Powsil Burns (Pl. 5). Secondary sites of *S. variegatum*



Fingland Burn, 600 ft. Fast torrential stream, 8-10 ft. wide, poor in water plants.
Simulium monticola, *S. variegatum* and *S. tuberosum*.

in the larger streams of valleys were mentioned by Edwards (1920) and by Smart (1944) and our records support their opinions (Table 10, nos. 3, 4, 6, 7, 8, 14, 15, 17, 62, 86, 88, 89, 90). *S. variegatum* does not accompany *S. monticola* in small hill-streams, and this might have led Edwards, Oldroyd & Smart (1939) to conclude that the two species are not found together, though their general habitat is similar. *S. variegatum* shows a preference for colonizing water-washed stones (Water of Leith, Haugh Head; compare species composition of A, B and C in Table 5, p. 40). When, however, the surfaces of stones are

(4) *Simulium reptans*

For some unknown reason this species does not appear to inhabit the hill streams in which *S. variegatum* is found. Only a scanty population was occasionally found in the Fingland Burn together with *S. monticola* and *S. variegatum* (Table 12), and this may lead to the assumption that in some cases individual females may not be successful in finding their primary sites and may deposit their eggs in an unusual secondary habitat. Its confinement to the larger semi-upland streams and main drainage basins,

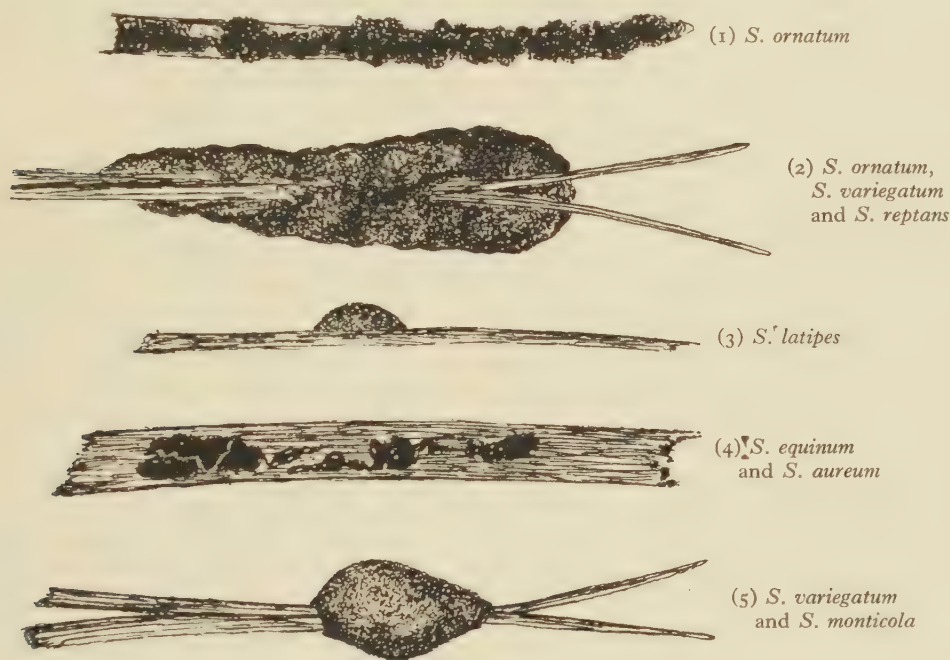


Fig. 1. Egg masses of different species ($\times \frac{1}{2}$): (1) irregular shape, several layers of eggs; (2) cake-like, several layers of eggs; (3) very small heaped mass, several layers; (4) small batches of few layers; eggs laid vertically; (5) small compact heap, ball or cake-like.

unsuitable because of sedimentary deposits, etc., the majority of the larval colonies are found on vegetation (cf. egg mass, Fig. 1 (5), as in North Esk, Carlops). In secondary habitats *S. variegatum*, unlike *S. reptans*, does not extend its larval distribution into the lowlands. This was remarked in August 1946 in the Whiteadder Water where *S. variegatum* was associated with *S. reptans* and *S. ornatum* in the semi-upland area (Table 10, nos. 86–90), but its numbers gradually decreased downstream until it completely disappeared near Blannerne House (Table 10, no. 91). Here the other two species occurred in abundance with *S. equinum* in the smoother but slower current.

where its larval colonies occur both on vegetation and stones, would justify its classification as a true riverine species (Table 10, nos. 3, 4, 6, 7, 8, 14, 15, 17, 62, 88, 89, 90, 91). In regard to its association with *S. variegatum* and *S. ornatum*, the three may share one and the same oviposition site, and there is one instance in which a female of each species was found affixed to the gelatinous matrix of what was evidently a common egg-mass on the leaf of a plant in the North Esk at Carlops in the summer of 1946 (Fig. 1 (2)). In June of this same summer, larval colonies of *S. reptans* in pure culture on stones were recovered from the river Devon, Kinross (Table 11, no. 95), the only

occasion on which we found the larvae unaccompanied by any other *Simulium* species.

The variety *galeratum* of *S. reptans* which Edwards (1920) described, has been found to occur in variable numbers in all *S. reptans* colonies. Its separation from the parent species is by no means clearly defined and the presence of numerous intermediate forms would indicate that *galeratum* has not so far achieved stability. Similar larval variations have been found to occur in other species of *Simulium*. According to Pentelov (1935) and Butcher *et al.* (1937), the larvae of *galeratum* are said to occur on the leaves of aquatic plants; but in the Water of Leith at Haugh Head it was found along with typical *S. reptans* on the surface of water-washed stones.

(5) *Simulium latipes*

The larvae of this species are variously found in mountain rills, small stony or gravel-bottomed hill streams and sometimes in lowland streams and small rivers. Actually its breeding places are confined to the waters of the first two, since it is usually in these that it lays its eggs (Fig. 1 (3)). In tiny rills its larvae may be the only *Simulium* species represented; but in stony-bedded hill streams it is accompanied by *S. monticola* and again by *S. ornatum* in such as are gravel-bottomed and fringed with plentiful vegetation (Table 19). Its invasion of lowland streams is explained by larval migration from hill streams as a result of desiccation or flooding. An excellent example of the former was observed in August 1947. In collections of the *Simulium* larval population taken from the semi-upland Whiteadder at Hungry Snout (Table 10, no. 88) it was found that *S. latipes*, an unusual intruder, accounted for 13 % of the total community, which otherwise consisted of *S. reptans*, *S. variegatum*, *S. ornatum* and *S. aureum* (Table 18).

As to whether *S. latipes*, apart from migration, can successfully survive absolute desiccation in the beds of dried-up hill streams is a question which has not been solved. In this respect we may suggest that during dry seasons this species breeds in medium-sized hill streams which do not completely dry up. This was evidenced by the presence of its egg-masses in such streams in summer. The presence of early instar larvae about Christmas in streamlets that had been dry the previous summer led Edwards *et al.* (1939) to accept the suggestion of Ussing (1925) that the eggs withstood drying. Presumably they proceeded to hatch with the resumption of the flow of water. The more probable explanation, which Edwards overlooked, is that the larvae hatched from eggs of the second generation laid in autumn under normal stream conditions. We ourselves have collected recently deposited egg-masses in upland streams as late as the end of October (1946).

(6) *Simulium tuberosum*

According to Edwards (1920), this is a species of which the larvae, in company with those of *S. reptans*, occur on stones in rapid rivers. Undoubtedly, this is not its primary habitat but rather the smaller rapid hill streams, which it shares with *S. monticola* and *S. variegatum* and where its presence was denied by Edwards. Like *S. variegatum* the larvae of *S. tuberosum* may make their way downstream to connecting rivers, but usually no farther than their upper reaches. Thus it was recovered with *S. reptans* from the River Varragill, Skye, in May 1947, and, similarly, the two have been reported from the Upper Tees by Butcher *et al.* (1937). As a pure culture, a sparse population of *S. tuberosum* was found once in the March Burn, Kilsyth Hills, Stirlingshire (Table 11, no. 93), in May 1946.

(7) *Simulium aureum*

Of this species, Edwards *et al.* (1939) remark that it is not an uncommon British species but one that is easily overlooked. Edwards, too, states that its life history is similar to that of *S. latipes* and that the larvae occur in small streams and rills like those of *S. latipes*. As regards these opinions our experience is at variance with that of Edwards. In the first place, the larvae of *S. aureum* were mainly recovered from sizeable semi-upland and lowland streams (Table 10, nos. 80, 81). The only record of the presence of *S. aureum* in small streams was from the Mill Lade, Traquair, Peeblesshire, a stream in which *S. ornatum* is the commonest breeder but the occurrence of *S. latipes* very casual and irregular (Table 13).*

In Berwickshire, a few larvae were first encountered in the Blackadder at Nisbet Hill in the summer of 1946, in a large mixed association of *S. ornatum* and *S. equinum*. Examination of this locality (Nisbet Hill), (Table 20) in 1947 showed that all three species were again present, but whilst the numbers of *S. aureum* had appreciably increased, those of *S. equinum* were much reduced. In this year, too, it was found in Langton Burn, Gavinton, a tributary of the Blackadder (Table 21) and also at other stations farther up the Blackadder (Tables 22–26). At these latter stations whole populations of *S. ornatum* and

* Here three pupae of *S. aureum* were found on 1 May 1946 in a sample of 200 pupae whose composition was 3 *S. aureum*, 1 *S. latipes*, 12 *S. monticola*, 24 *S. variegatum* and 160 *S. ornatum*. Again on 16 of July 1946, in the same stream, *S. aureum* formed 15 % of total larval-pupal population, which was mainly *S. ornatum* with an odd number of *S. monticola*. In 1947, *S. aureum* appeared in the Mill Lade in August, forming 1.5 % of the total larval-pupal population which was 79 % *S. ornatum*, 14.5 % *S. latipes* and 5 % an undetermined *Simulium* (small larvae).

Table 19. *Percentage species composition of Kettelshiel Burn, Kettelshiel, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. latipes</i>	<i>Simulium</i> undet.	Total no. in all samples
May	44	5	51	.	50
July	15	.	2	83	910
Aug.	96	.	4	.	755
Sept.	98	.	2	.	906

Table 20. *Percentage species composition of Blackadder, Nisbet Hill, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. reptans</i>	<i>S. venustum</i>	<i>S. equinum</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	23	2	62	11	2	.	.	63
June	65	.	*	.	4	1	30	8074
July	60	.	.	.	1	5	34	2610
Aug.	58	.	.	.	.	22	20	1436
Sept.	.	.	.	.	.	egg masses	.	.

* Only two pupae were collected.

Table 21. *Percentage species composition of Langton Burn, Gavinton, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. latipes</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	8	89	3	.	.	76
July	63	2	.	.	35	1415
Aug.	100	.	.	.	.	417
Sept.	97	.	.	3	.	270

Table 22. *Percentage species composition of Wedderlie Burn, Westruther, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. latipes</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	63	27	10	.	.	82
July	84	9	1	.	6	1993
Aug.	Egg masses	.	.	Egg masses	.	.
Sept.	16	.	.	42	42	1911

Table 23. *Species composition of Blackadder, Hallyburton, summer 1947*

Date	<i>S. ornatum</i>	<i>S. monticola</i>	<i>S. venustum</i>	<i>S. aureum</i>	<i>S. equinum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	2	1	97	.	.	.	433
June	10	.	.	.	2	88	3272
July	Egg masses	.	.	Egg masses	.	.	.
Aug.	.	.	.	100	.	.	1187
Sept.	.	.	.	100	.	.	138

Table 24. *Percentage species composition of Gordonmains Burn, Greenlaw, summer 1947*

Date	<i>S. ornatum</i>	<i>S. latipes</i>	<i>S. venustum</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	62	9	29	.	.	213
June	.	.	.	.	.	.
July	.	.	.	.	.	.
Aug.	28	.	.	2	70	400
Sept.	96	.	.	4	.	525

Table 25. *Percentage species composition of Blackadder, Greenlaw, summer 1947*

Date	<i>S. ornatum</i>	<i>S. variegatum</i>	<i>S. reptans</i>	<i>S. venustum</i>	<i>S. aureum</i>	<i>Simulium</i> undet.	Total no. in all samples
May	.	21	29	50	.	.	28
June	.	.	4	.	.	96	506
July	48	7	1	.	44	.	583
Aug.	45	.	.	.	55	.	510
Sept.	36	8	.	.	56	.	237

Table 26. *Percentage species composition of Blackadder Water, Castle Mill, summer 1947*

Date	<i>S. ornatum</i>	<i>S. variegatum</i>	<i>S. venustum</i>	<i>S. reptans</i>	<i>S. aureum</i>	<i>S. equinum</i>	<i>Simulium</i> undet.	Total no. in all samples
22 May	33	14	32	21	.	.	.	38
1 July	72	.	.	1	.	2	25	6696
1 Aug.	.	.	.	.	.	.	.	.
26 Aug.	72	.	.	.	27	1	.	2624
23 Sept.	97	.	.	.	3	.	.	432

S. aureum disappeared. This is possibly explained by larval migration due to algal overgrowth of the substrata and accumulation of silt under low-water conditions.

As an illustration of the irregular annual occurrence of *S. aureum*, it should be noted that whilst the species was recovered in 1947 from Langton Burn, Gavinton Water and also from the upper Whiteadder at Hungry Snout (Table 18) along with *S. reptans*, *S. variegatum* and *S. ornatum*, in both streams it was absent in 1946. Later the larvae were collected from stones in Boondreich Water, near Thirlestane in the same country (Table 11, no. 68).

Table 27. *Percentage fluctuation in populations of S. monticola and S. variegatum in Fingland Burn*

	<i>S. monticola</i>	<i>S. variegatum</i>
Spring 1945	37	63
Summer 1945	50	50
Spring 1946	25	75
Summer 1946	2	98
Spring 1947	94	6
Summer 1947	87	12*
Spring 1948	78	22

* and 1% *S. reptans*.

Due attention was paid to its possible occurrence with *S. latipes* in its primary habitat of small hill streams, but our quest proved negative. It is curious that despite the fact that females of *S. aureum* were observed ovipositing (Fig. 1 (4)) in the Blackadder at Nisbet Hill in September 1947, larvae have not so far (July) been recovered in this stream in 1948, but, on the other hand, larvae of *S. reptans* only scantily recorded in the spring of 1947, appeared in abundance in 1948. *S. aureum* presents a good example of the peculiar lack of constancy in the components of a *Simulium* association from year to year. One year a species may be strongly represented at a particular

site, whilst it may be entirely absent or very scanty the following year. An excellent example of this seasonal fluctuation came to our notice from Fingland Burn, Traquair, where *S. monticola* and *S. variegatum* permanently breed (Table 27).

(8) *Simulium equinum*

There is little to remark about this species save that it breeds mainly in rivers, like *S. aureum*. In the course of our survey it was found breeding in the Blackadder, Whiteadder and Leader Water, Lauder (Table 11, no. 67), Berwickshire, and again in the River Tyne, East Lothian (Table 11, no. 47), from which latter county it had been previously recorded by Edwards *et al.* (1939). The egg-mass is shown in Fig. 1 (4)).

(9) *Simulium venustum*

This species was recorded by Edwards (1920), Edwards *et al.* (1939) and Smart (1944) as a lowland species confined to the south and south-east of England, where the larvae occur in weedy rivers of moderate current. In the present investigation it was recorded at Dinnet, Aberdeenshire (Table 11, no. 131) in a small stream on 23 September 1946, and again at Hallyburton (Table 23) and Greenlaw (Tables 24, 25) in the Blackadder, Berwickshire, on 24 May 1947, but did not appear later. These two records would seem to be the first for the species in Scotland.

(10) *Simulium nollerii*

According to Edwards *et al.* (1939) and Smart (1944) this species is localized in Wales and the southern half of England. Our collection from Schochie Burn, Perthshire (Table 11, no. 100), on 22 September 1946, seems to be the first record for Scotland. Larvae and pupae were found there in association with those of *S. ornatum*, *S. reptans* and *S. latipes*.

4. GENERAL BIOLOGY

(a) Hibernation

It is commonly accepted that some Simuliidae hibernate in the larval stage, and the following species are known to belong to this class: *S. ornatum*, *S. variegatum*, *S. monticola*, *S. latipes* and *S. equinum*.

There is however, circumstantial evidence that overwintering as ova may occur in *S. reptans* and *S. tuberosum*. This evidence rests on the absence of their larvae and pupae from streams in winter, and also of adults at this season.

Owing to the absence of data on *S. aureum* and *S. venustum* in winter, in places where their larvae were encountered in summer, the question of their hibernation has not so far been solved.

the larvae, which have been found alive at depths of 3-9 in. under ice, attached to the stems and leaves of *Juncus*, *Agrostis* and withering leaves of *Phalaris* and *Carex*. Of these, *Juncus* was colonized by larger numbers of the larvae in winter. Contrary to Smart's experience (1934) with *Simulium ornatum*, which migrated from the withering leaves of *Glyceria fluitans* to stones in the stream bed in winter, we found that this species, at all stations on the Water of Leith, retained its association with *Juncus* and other green vegetation all winter, and very few larvae were then found on stones (Table 28).

Even *Simulium variegatum* and *S. monticola*, which normally inhabit stones in cascades in summer, seemed to prefer *Juncus* and other green vegetation such as *Agrostis* in winter for their support. However,

Table 28. *Simulium* population in winter and summer at site IV, Water of Leith, Haugh Head*

	Larvae per sq.ft. of vegetation		No. of populated stones out of 10 examined	Remarks
	Site IV A	Site IV B		
Dec. 1946	416	208	3	Total number on each stone: 30, 20 and 9.
Jan. 1947	540	180	3	Total on each stone: 5, 11 and 15
Apr. 1947	612	185	.	
May 1947	700	350	5	18-20 per sq.in.
Aug. 1947	1974	1462	7	88-133 per sq.in.

* The species involved here are: December and January, *S. ornatum* and *S. variegatum*; April to August, *S. ornatum*, *S. variegatum* and *S. reptans*

Regarding the species that hibernate as larvae, Smart (1934a) in his work on *S. ornatum* in the Braid Burn, Edinburgh, showed that this species is a good example and we have been able to substantiate his conclusions in various other streams in which *S. ornatum* breeds. The same mode of hibernation also applies to *S. variegatum*, *S. monticola*, *S. latipes* and *S. equinum*. From the middle of October to the beginning of November larvae of different stages are regularly found in streams and frequently, too, the egg-masses of *S. ornatum* that have been recently laid by females of the third generation. Females of *S. ornatum*, for instance, may occur late in the autumn and have been collected feeding on cattle as late as the third week of October.

Concerning the instar components of larval colonies in the autumn, it would appear that those that are full grown are individuals of the second generation in which development has been retarded by parasitic Protozoa (*Thelohania*, *Serumsporidium*) or parasitic nematodes (*Mermis*) and that they ultimately succumb to infection without succeeding to pupate. Early stage and half-grown larvae are those which survive, and although their development is slow compared to the summer generations, it nevertheless proceeds even in water with a temperature no higher than 6° C. Freezing temperatures do not appear to inconvenience

alternative winter sites may not always be available, e.g. in the Westquarter Burn (Stirlingshire) (p. 48), where larvae of *Simulium ornatum* must perforce utilize stones for their anchorage in summer and winter.

In the depths of winter when the smaller streams may become covered with ice, hibernating larvae were recovered on vegetation below the ice. Under these conditions of low temperature, 4° C., the feeding activities, and therefore the growth, of the larvae are retarded; but that development is not entirely suspended is shown by the occurrence of recently moulted larvae in samples taken from streams in winter, when the temperature of the water was 1-3° C. Examination of larval samples collected periodically during the winter revealed a steady reduction in the numbers of early instars and a comparable increase of the more mature, culminating in the production of pupae in February at a temperature of 4-6° C.

To test the effect of low temperature on larval development under controlled conditions, samples of 12 larvae of third to penultimate instars of a mixture of *S. monticola*, *S. variegatum* and *S. ornatum* were placed in water in glass tubes, provided with a culture of plankton from the stream in which larvae naturally existed. The tubes were introduced to a refrigerator at a temperature of 1.7° C. and under these conditions

moulting and pupation were found to occur in 3–12 days after the experiment commenced (1 March 1948). The results, therefore, serve to confirm the events of larval development as they occur in winter in nature and show that such development can occur at temperatures close to zero.

It was noted that in winter the gut of hibernating larvae was either only partly full or else entirely empty.

(b) Generations

The date of emergence of the spring generation of species which hibernate as larvae depends on the temperature of the water during winter and spring. The rate of larval growth varies directly with rise of temperature, and the intervention of milder spells of weather during the cold season serves to accelerate the development of the larvae, some of which proceed to pupate about the middle of February. Indeed, pupation may occur at temperatures around 0° C., a fact which was confirmed by our refrigerator experiment (1.7° C.) and field observations in 1948, when pupae of *S. ornatum* were collected from the Mill Lade, Traquair, in February with water temperature at 3° C. and 1 March at 4.1° C. after a period of frosty weather (the mean of air temperature during 23–29 February was 1.8° C. Edwards, too, had previously recorded the occurrence of pupae in February immediately after frost. In comparison with the winter of 1946 and 1948, that of 1947 was much more severe, being characterized by a prolonged period of freezing, which extended from the end of January to the end of March. As a result, pupation in larval populations in streams was delayed, and the first pupae did not appear in our collections until the middle of April.

The duration of the pupal stage was, likewise, found to vary with the temperature. To determine the duration of pupal stage, a sample of 1500 *S. ornatum* larvae was taken from a stream in February 1948, and transferred to the laboratory for rearing in a special apparatus. The temperature of the water was recorded twice daily, and pupae as they were formed were counted daily and records of hatching were also kept. The duration of the pupal stage was found to vary with the temperature as shown in Table 29 and Fig. 2.

From these results we find that in pupae bred at temperatures under 6 and 7° C. the period of development averaged 17 days, but this was reduced to 7–8 days at 9.6° C. A few pupae kept in a refrigerator at 1.7° C. remained unhatched for 4 weeks, but when transferred to an incubator at 10° C. they hatched to flies in 3–4 days. Evidently development, although retarded, had been slowly proceeding even during refrigeration and this prolonged submission to temperatures near freezing appeared to accelerate the development of the pupae when returned to the higher temperature.

Expression of the effect of seasonal stream temperatures 6–10° C. on the time of pupation and adult emergence was noted from year to year. In 1946 it was observed that in combined colonies of *S. ornatum*, *S. variegatum* and *S. monticola* mass pupation and emergence of the overwintering generation occurred at the beginning of April at a water temperature of 11.5° C. In 1947 pupation started 2 weeks later and mass emergence was observed about the beginning of May, whilst in 1948 the process was more irregular and prolonged so that pupae and adults apparently appeared in batches from March onwards to the second and third week of April, when the last batch emerged. This spread in the time of emergence was possibly associated with greater temperature fluctuations during the winter and spring of this year. In all cases of mass pupation and emergence the temperature of the water was about 10° C. and the air temperature from a minimum of 4.4° C. to a maximum of 10° C. In 1948, however, the minimum was 3.7° C. and the maximum 11.6° C.

Among the species that hibernate as larvae *S. ornatum* is more precocious than the others in pupating in spring. The first pupae may appear as early as mid-February, although the bulk emergence of its adults coincides with that of *S. variegatum* and *S. monticola*. As far as *S. latipes* is concerned, this larval hibernator appears on the wing in May and June when it overlaps *S. reptans* and *S. tuberosum*, which, we presume, hibernate in the egg. Evidence regarding the mode of overwintering of these two seems to permit of no other interpretation, since the earliest active stages to appear in streams are the first and second larval instars about the middle of March* which reach full growth in 5 or 6 weeks and produce the first generation of flies about the beginning of May or the beginning of June. Edwards (1920) also remarked that these two species do not appear until the end of May or beginning of June.

The summer generation usually overlaps with the spring and autumn generations. Thus, egg-masses of early individuals of the spring generation of *S. ornatum* were obtained at Traquair in May 1946 along with some late larvae and pupae of the spring generation; and again in Water of Leith, Haugh Head, on 25 May 1947. In other streams the presence of first, second and third instar larvae shortly after the emergence of the spring generation indicated that they were laid sometime during the emergence of the latter. But this should not be taken as the rule, for the early emerging individuals of the spring generation may be faced with unfavourable weather conditions and thus egg-laying may be postponed, as occurred in 1948, when no egg-masses were recovered from any stream

* In 1947 first instar larvae appeared about the second week of April.

Table 29. *Duration of pupal stage*

(Mean temperatures of the periods through which these pupae passed their life are given in Fig. 2.)

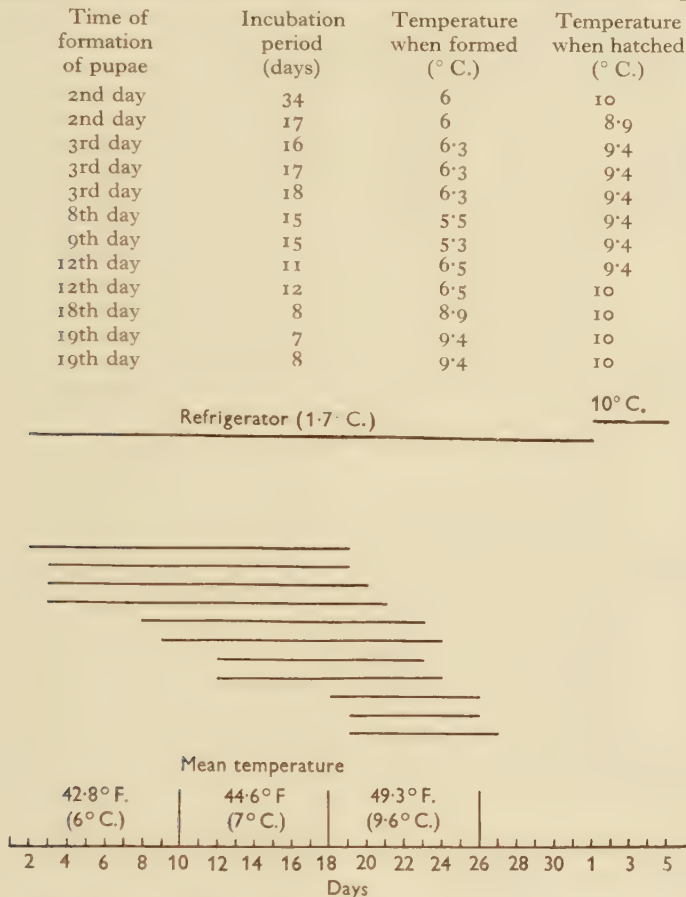


Fig. 2. Duration of the pupal stage under experimental conditions.

until the beginning of May. Regarding the laying period of the first generation our experience is at variance with that of Smart (1934a) who assumed that the period of egg-laying extends over a period corresponding to that over which pupation extends. As has already been stated, adult activity may be delayed by adverse weather conditions, which may have no effect on pupation and emergence as long as the temperature is high enough for the purpose. In other words, there is no relation between the laying and pupation periods since the two occur at different stages of the developmental process. Further, it has been noted that after a period of weather favourable for adult activity, egg-masses were more abundant than they were after windy and wet conditions.

The time of appearance of the bulk of the summer generation of *S. ornatum*, *S. monticola*, *S. variegatum*, *S. latipes* and *S. equinum* may be either July or August.

In 1946, in which year the spring generation appeared in April, mass pupation and emergence of the summer generation was observed in July, while in 1947, when the spring generation was delayed till May, the summer generation did not appear until August. The summer generation of *S. reptans* (egg-hibernator) in 1946 appeared 2-3 weeks later than that of larval hibernating species, but in 1947 it appeared about the same time as other species. This, probably, was due to the warm weather which prevailed in the summer of 1947, and speeded up development of all species particularly *S. reptans*, which has a comparatively short larval life.

A summer generation of *S. tuberosum* and *S. venustum* was not encountered, and we may infer that these species, unlike *S. reptans*, are univoltine.

An autumn generation of *S. ornatum* was encountered in 1946 in stretches of streams near the

lowland, such as Murrieston Water and Linhouse Water, Midcalder, where abundance of mature larvae was recovered about the end of August, and possibly these larvae were ready to pupate about the first half of September. Again in 1947, in the Westquarter Burn, an autumn generation of *S. ornatum* was discovered about the end of September and beginning of October.

An autumn generation was generally absent in upland streams, for the number of mature larvae and pupae present in September and October in these streams was so small that it would be reasonable to consider them late individuals of the summer generation.

As regards the irregularities of development of larvae in hill streams, we can confirm Smart's experience (1936) at Fortingal, where he found it difficult to trace the development of *S. latipes* and *S. ornatum*. Irregularities may be attributable to certain peculiarities of hill streams, such as lower temperature and poverty of plankton.

As regards *S. aureum*, our experience, similar to that of Edwards (1920), is unsatisfactory because of the variability of its occurrence. From evidence obtained from the Blackadder it would appear that there are at least two annual generations, a summer one and an autumn one, with a possibility of a third or spring generation, of which there was some evidence at Traquair (Mill Lade). But the few larvae of *S. aureum* collected in spring (March 1948) were parasitized by *Mermis* and *Sporozoa* and may have been a remainder of the autumn generation, the development of which had been retarded by parasitism.

(c) Economic position of the Simuliidae

In Scotland the Simuliidae, according to Edwards, are represented by some twelve species, of which nine here or elsewhere are known to feed on the blood of man and domestic animals. Actually, during the course of the present investigation, only four Scottish species were recorded as blood-sucking, namely *S. reptans*, *S. ornatum*, *S. variegatum* and *S. monticola*. Neither in density of numbers nor in pathogenic effects on their hosts does any of them bear comparison with the notorious Danubian golubatz fly (*S. columbaschense* (Schoü)) or the Southern buffalo gnat (*S. pecuarum* Riley), to which reference is made by Edwards *et al.* (1939); or again to the Canadian cattle black-fly (*S. arcticum* Mall), the habits of which were first described by Cameron (1922) and recently by Rempel & Arnason (1947). The latter record serious losses of cattle and other livestock due to mass attacks of this species. In Canada, too, there are vast stretches of territory, particularly in Northern Ontario, where the black-fly, *S. venustum* Say, makes

life almost unbearable to human beings during the summer season.

So far as the human host is concerned, black-flies in Scotland have a nuisance value that must be rated of minor importance compared with that of blood-sucking midges of the genus *Culicoidee*. In the Edinburgh district black-fly attacks on human beings are usually recorded in the spring (April) and are identified not with *S. ornatum*, which chiefly feeds on cattle, but with *S. reptans*. Both species are breeding associates of the Water of Leith, which flows through the City of Edinburgh, as well as of other Scottish streams, some of which have already been noted.

To supplement our scanty knowledge of the association of black-flies with livestock, twelve farms (Table 30), distributed in the counties of Stirling (2), Midlothian (3), Peebles (1) and Berwick (6), were selected, and periodic examinations of cattle and horses at pasture were made during part of the fly season (June to October) in 1947 and again in 1948. Of the four *Simulium* species collected, *S. ornatum* was the most frequent. On two Stirlingshire farms *S. ornatum* was the only black-fly found on stock, and its origin was traced to the Westquarter Burn at Laurieston, where it bred prolifically. In Midlothian *S. reptans*, as well as *S. ornatum*, was found on cattle at farms adjoining the Water of Leith where these species were known to be common breeders. At one Peeblesshire farm kept under observation, *S. ornatum*, *S. reptans*, *S. monticola* and *S. variegatum* were found on cattle, and in one instance, in October 1947, all four were taken feeding on a single cow. It is somewhat surprising that neither *S. aureum* nor *S. equinum*, which bred in the Blackadder, were recorded on either horse or cattle during this investigation.

Black-fly attacks are usually confined to the under-surface of the body of horses and equines but they may extend their feeding operations to include the dewlap and the lower lip. The most common local symptom that accompanies the bite-punctures of *S. ornatum* is an oedematous swelling of the udder in cattle and the sheath in bullocks and horses, and this is usually more apparent during the period of activity of the spring generation of flies than of the later ones. The biting of the flies appears to continue during most hours of daylight, equally on bright or overcast days, and is most intense under conditions of high relative humidity at temperatures ranging from 10° C. to almost 26.7° C.

In the literature, *S. ornatum* has been reported as occasionally biting man (Edwards *et al.* 1939), but we have never known it to do so, even under circumstances in the field where this could readily have happened in the vicinity of cattle. Attempts were made to induce impregnated wild flies, captured in field, to feed on human beings, both in the laboratory as well as out of doors, but with no success. The

Table 30. *Simulium blood-sucking records*

Species	No. of flies	Time spent in collection (min.)	Host	District	Date	Time of observations (p.m.)	Temperature (° C.)	Weather
Stirlingshire:								
<i>S. ornatum</i>	.	.	Bullocks	Mumrills	13. vi. 47	5-6	13	Dull, occasional drizzle
<i>S. ornatum</i>	24	10	Cow	Mumrills	14. vii. 47	5-6	15	Sunny, warm, slightly breezy
<i>S. ornatum</i>	40	15	Cow	Mumrills	14. viii. 48	8-9	20	Warm, slight breeze
<i>S. ornatum</i>	65	5	Cow	Mumrills	27. viii. 48	5-6	22	Warm, slight breeze
.	.	.	.	.	16. ix. 48	4-5	.	Windy, rainy, occasional sunshine
<i>S. ornatum</i>	250	10	Cow	Mumrills	5. x. 47	6-7	12	Fair, cool in the afternoon
<i>S. ornatum</i>	10	15	Cow	Mumrills	23. x. 47	5-6	10	Fair, slightly breezy cool
Midlothian:								
<i>S. reptans</i>	6	10	Cow	Whelpside	15. viii. 47	7-9	20	Warm, slight breeze
<i>S. ornatum</i>	16			Haugh Head	15. viii. 47	1-3	23	Warm, sunny
	None	.	.	Aimville and East Haugh				
<i>S. reptans</i>	2	15	Cow	Haugh Head	27. viii. 47	1-2	23	Very warm, sunny
<i>S. reptans</i>	2	15	Cow	Whelpside	27. viii. 47	1-2	23	Very warm, sunny
<i>S. ornatum</i>	3	15	Cow	Haugh Head	17. ix. 47	5-6	11	Wet and windy in forenoon, dry and quiet in the afternoon
Peeblesshire:								
<i>S. reptans</i>	31	5	Cow	Traquair	5. viii. 47	7.30-9.30	19.5	Very warm till 4 p.m. then breezy later
<i>S. monticola</i>	5			Knowe				
<i>S. ornatum</i>	4	.	.	Traquair	10. ix. 47	5	11	Windy, showery, cool
	.	.	.	Knowe				
<i>S. ornatum</i>	16	30	Cow	Traquair	4. x. 47	4.30-5.30	15	Windy, showery in forenoon, quiet and mild in the afternoon
<i>S. monticola</i>	4			Knowe				
<i>S. reptans</i>	8							
<i>S. variegatum</i>	1							
Berwickshire:								
<i>S. ornatum</i>	12	15	Cow	Greenlawdean	25. viii. 47	6-7	18	Sunny, warm, but breezy later
<i>S. ornatum</i>	1	30	Horse, Cow and Sheep inspected	Castle Mill	26. viii. 47	1-2	23	Very warm, sunny
<i>S. ornatum</i>	6	15	Cow	Mountcastle	26. viii. 47	4-5	22	Very warm, sunny
<i>S. ornatum</i>	20	15	Cow	Caldra	26. viii. 47	6.30-7.30	19	Cooler
<i>S. ornatum</i>	25	15	Horse	Caldra	26. viii. 47	6.30-7.30	19	.
<i>S. ornatum</i>	15	15	Cow	Nisbet Hill	26. ix. 47	5-6	13	Cloudy, quiet
<i>S. ornatum</i>	6	15	Horse	Caldra	26. ix. 47	6-7	12	Same
<i>S. ornatum</i>	2	15	Horse	Caldra	1. xi. 47	4-5	12	Changeable, showery, bright intervals
Peeblesshire:								
<i>S. variegatum</i>	17	10	Cow	Traquair	3. vii. 48	9-10	14	Cloudy and breezy in the forenoon, quieter and brighter later.
<i>S. monticola</i>	7			Knowe				
<i>S. reptans</i>	6							
Berwickshire:								
<i>S. ornatum</i>	12	10	Horse	Fogorig	9. vii. 48	1-2	16	Warm, quiet
<i>S. reptans</i>	26							

same applies to our efforts to feed flies confined in small cages on warm defibrinated blood; nor did they show any interest in feeding when exposed on the ears of laboratory rabbits, which are readily acceptable to mosquitoes, clegs and stable flies. Laboratory-reared females of *S. ornatum* proved even more refractory in experimental feeding than did wild specimens. In the Nematocera it is only after mating and impregnation that the female seeks a blood meal. As a rule mating occurs at swarming out of doors (eurygamy), and since in the Simuliidae the sexes were found not to mate in the narrow confined space of a cage in the laboratory (stenogamy), we anticipated, as events later proved, even less chance of success in inducing unmated females to bite a human or rodent host in the laboratory. Indeed, it is well known that black-flies which have begun to feed on cattle out-of-doors readily abandon their hosts as they pass into a barn under cover or shortly after they have entered.

5. ACKNOWLEDGEMENTS

The investigation was carried out under the terms of a Research Scholarship awarded by the Egyptian Ministry of Public Health 1945-9, at the Department of Entomology, University of Edinburgh, under the supervision of Dr A. E. Cameron, Reader in Entomology, who selected the problem and planned the investigation. I am deeply indebted to him for his kindness in providing accommodation and facilities in his department, for his close supervision, helpful criticism and continued interest and encouragement. My grateful thanks are extended to members of his staff who gave valuable assistance as the investigation proceeded, especially Dr J. Allan Campbell who offered kind advice in the construction of the rearing apparatus. I also thank Mr Myles Crooke for his assistance in the summer survey of 1946.

Thanks are due for their helpful advice, to Dr E. Wyllie Fenton and Dr A. M. Smith of the Edinburgh and East of Scotland College of Agriculture, on the botanical and chemical aspects respectively.

I am grateful for help received from Mr Buckpit, County Organizer, Berwickshire, and from farmers in different parts of Scotland (particularly Mr S. Smith, Laurieston, Stirlingshire, and Mr G. Scott, Traquair, Peeblesshire) for providing facilities through which blood sucking records were obtained.

I am much indebted to Mr C. Elton, Bureau of Animal Population, Oxford, for his valuable suggestions during the preparation of this manuscript for publication.

6. SUMMARY

1. An account is given of the distribution of the Simuliidae in south-east Scotland. *Simulium tuberosum*, *S. latipes* and *S. monticola* inhabit upland streams;

S. tuberosum, *S. variegatum* and *S. reptans* semi-upland ones, and *S. ornatum* is widely distributed in all regions. *S. aureum* and *S. equinum* were encountered in abundance in fairly large semi-upland and lowland streams. Occasional records only were obtained of the distribution of *S. venustum* and *S. nollerii*.

2. Within their appropriate regions the different species exhibit a different choice of habitat. Thus, *S. latipes* is found in ditches and small streams, and when these habitats are dried up in summer, eggs are sometimes deposited in medium-sized hill streams. *S. monticola* is found in hill-streams (feeders). *S. variegatum* and *S. tuberosum* are inhabitants of tributaries as well as main drainage rivers. *S. reptans* is a true riverine species.

3. Distribution depends primarily on the selection of site by the gravid female. From the primary sites established by the deposition of egg masses, larvae may migrate actively to secondary sites, either in response to unfavourable conditions such as desiccation, or they may be carried passively during conditions of spate. Gravid females of different species (e.g. *S. ornatum*, *S. variegatum* and *S. reptans*) may share a common site for egg-laying, thus forming a primary focus of the three species.

4. *Simulium* associations were studied in many streams of south-east Scotland.

5. The principal environmental factors affecting the habitat of the immature stages of Simuliidae are: (1) temperature of the water, (2) type of current, (3) current rate, (4) vegetation, (5) characters of stream bed, (6) food material and oxygen. The relative importance of these factors is discussed.

6. The size of *Simulium* pupae depends upon the availability of food material during larval existence. When plankton is less abundant (e.g. during drought) pupae are smaller.

7. There is no direct correlation between current velocity and degree of oxygen saturation, and it is concluded that the relation of *Simulium* to current is not determined through the oxygen factor. (Physical conditions of the substrata have a pronounced effect in limiting larval distribution.) Accumulation of silt and overgrowth by bryophytes compel larval migration, and these conditions occur most readily when the current rate is slow.

8. It was difficult to determine the density of population accurately in different streams. Approximate comparison was only achieved by observations at chosen sites.

9. Hibernation of *S. ornatum*, *S. variegatum*, *S. monticola*, *S. latipes* and *S. equinum* occurs in the larval stage.

10. Development of larvae in winter is accelerated with rise of temperature during intervening mild spells. In mild winters pupation occurs as early as

mid-February, but the duration of the pupal stage is prolonged so long as the temperature is low. Mass pupation and emergence of the spring generation occurs when the water temperature is about 10°C.

11. The summer generation appears in August and July, the autumn generation in September and October. (The species, *S. tuberosum* and *S. venustum* are probably univoltine, whilst *S. monticola*, *S. variegatum*, *S. reptans*, *S. latipes* are bivoltine. *S. aureum* and *S. equinum* probably have two or three generations per annum. *S. ornatum* in the lowland is trivoltine

but in the upland areas generally has two generations only. In this respect temperature plays a great role in influencing a species to develop two or three generations.

12. As blood-suckers *Simulium* species are less important in Scotland than in many other countries. They occasionally constitute a source of annoyance to humans. *S. reptans* is however frequently reported as troublesome in the Edinburgh district. Of the ten species included in the investigation only *S. ornatum*, *S. variegatum*, *S. monticola* and *S. reptans* were recorded biting cattle and horses.

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MIGRATION OF INSECTS AND BIRDS THROUGH A PYRENEAN PASS

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In our times the majestic phenomena of nature may still be admired, but rarely with that added zest, permitted to the ancients, of discovery. These things have been seen before, and additions to knowledge come nowadays from those who enumerate the ordinary at their backdoors. Once in a lifetime perhaps, the ecologist is translated back into a naturalist, through chancing on a spectacle which combines grandeur with novelty. Such was our fortune at the Port de Gavarnie on 13 October 1950.

The Port de Gavarnie is a narrow rocky pass, perhaps 50 yards wide, in the mountains which divide France from Spain, at about 7500 ft. above sea-level in the High Pyrenees. The main Gavarnie valley runs from the plains southwards for about 20 miles into the mountains; it has very steep sides and terminates in a huge Cirque of precipices 4000 and 5000 ft. high. The Port is 3 miles west of the Cirque, at the head of a subsidiary valley running up WSW. from the main valley through alpine meadows, with a final rather steep ascent over bare ground to the pass itself. 13 October was cloudless and sunny with a chill, fresh west wind. As we reached the divide at 11 a.m., a party of goldfinches fluttered past and dropped down on the other side into Spain. We soon realized that both birds and insects of various kinds were passing through WSW. on a considerable scale.

Small passerine birds came through in a succession of small parties, mainly of 5 to 15 individuals. Between 11.00 and 14.00 hr. (suntime), we counted 185 goldfinches (*Carduelis carduelis*), 402 chaffinches (*Fringilla coelebs*), 100 linnets (*Carduelis cannabina*), 34 serins (*Serinus canarius*), 23 meadowpipits (*Anthus pratensis*), 9 white wagtails (*Motacilla alba*) and 42 short-toed larks (*Calandrella brachydactyla*), in all 795 small passerines in 3 hr. It is unlikely that we missed many, as the pass is narrow and the birds flew low. The finches passed only just above the rocks, so that from where we sat low against a boulder, they often skimmed just over our heads. The pipits, larks and wagtails flew higher, mainly 6–20 ft. above us. It should perhaps be added that all these birds were migrating; none of them are resident at this spot, all were flying WSW. from France into Spain, and the steady flight of a migrant looks very different from normal flight.

Pigeons started passing just after midday, and at 14.00 hr. a compact flock of about 275 birds came through, some hitting the rocks with their wings as they breasted the pass, in the double fear of our unexpected presence and a pursuing peregrine falcon (*Falco peregrinus*). Including this party, 440 wood-pigeons (*Columba palumbus*) and 61 stock doves (*C. oenas*) passed in 2 hr. and we saw another hundred as we were descending later.

Butterflies were also travelling steadily through in the same direction as the birds, the numbers gradually increasing between 11.00 and 14.00 hr. Clouded yellows (*Colias croceus*)* were the commonest, particularly at first, but red admirals (*Vanessa atalanta*), which were scarcer at first, were nearly as abundant as clouded yellows at the end. We also saw a very small number of Bath whites (*Pontia daplidice*) and an extremely small number of pale-coloured clouded yellows (*Colias* sp.). (The butterflies, like the birds, were identified by sight.) All the butterflies flew steadily over the top of the pass against the wind, and then went down the other side. Most of them kept within a few inches of the ground, which made them difficult to pick up more than a few yards away. We did not count them, as we were counting the birds, but there were probably between 100 and 500 an hour, i.e. not a very big movement. A single hummingbird hawkmoth (*Macroglossum stellatarum*) was also seen near the top of the pass, but as it was not seen to cross, we are not sure whether it was migrating.

At 11.00 hr. dragonflies were passing through in numbers about double those of the butterflies, but after the first hour they became much more abundant, and at 14.00 hr. they were in very large numbers indeed, at least ten to every butterfly. Whenever we looked at right angles to the stream we could see at least six, and sometimes twenty, dragonflies in the air. They seemed to be passing at a rate of at least several thousand an hour, but they flew closer to the ground than did the butterflies and were very hard to see, so this may well have been an underestimate. All seemed to be of the same species, and the male and female which we collected were *Sympetrum striolatum striolatum*. The red males were at least ten times as abundant as the grey individuals (presumably females, but we would not have distinguished teneral males).

* The nomenclature followed for all European insects is that of Kloet & Hinks (1945).

Not until we had been at the pass for over an hour did we realize that another insect was migrating, so we do not know whether it was passing from the start. This was a hoverfly, the two collected specimens being males of *Episyrphus balteatus*. All the other individuals looked the same, and we have no reason to think that any other species was present. The syrphid flies, like the dragonflies, flew steadily forward WSW. against the wind, keeping extremely close to the ground, where the wind was, of course, weaker. Very occasionally one settled for a moment, but otherwise they travelled steadily onward. An estimate of numbers was impossible, but at a guess they were at least twenty times, and perhaps a hundred times, as numerous as the dragonflies. They were the most remarkable migrant of all.

OUR OTHER OBSERVATIONS

In 1950, we spent 10 days in various places high up in the Pyrenees. During this time, we saw enough to be able to say that small finches, swallows, pigeons and birds of prey regularly cross the high mountains on their southward migration (Lack, 1951*a*).

As regards butterflies, we saw another good passage south through the Col de Puymorens at 6000 ft. at the head of the Ariège valley in the eastern Pyrenees, between 11.00 and 15.00 hr. on 25 September 1950. There were probably about ten *Colias croceus* to every one of another species, but cabbage whites (*Pieris brassicae*) were fairly common, with small numbers of *Vanessa atalanta* and *Pontia daplidice*. They were flying south with a tailwind, keeping several feet above the ground, distinctly higher than at the Port de Gavarnie against the wind. The belt of moving butterflies was about half a mile wide, though the Col itself is several miles broad. The butterflies had very possibly been concentrated when coming up through the narrow Ariège valley a few miles back. (We have similarly seen chaffinches migrating on a narrow front through a wide valley because they had been concentrated by a geographical barrier 6 miles back.) After crossing the Col de Puymorens, the butterflies descended on the other side and we met them again 2000 ft. lower down near Spain.

On 30 September and 1 October, at the Col de la Quillane, between 5000 and 6000 ft., at the head of another southward-running valley, we saw a small number of *Colias croceus*, *Pieris brassicae* and *Vanessa atalanta* flying south, the weather being cold and misty, so presumably unfavourable. Finally on 11 October at the Port de Gavarnie, on a very chilly day with an east wind, a small but steady stream of *Colias croceus* came through WSW. with the wind, together with some *Pieris brassicae* and *Pontia daplidice*.

As regards dragonflies, we saw a few flying south on 1 October 1950, at the Col de la Quillane, and on 4 October 1947 one of us (E.L.) saw huge numbers, far more than at the Port de Gavarnie, flying south over the bracken slopes of La Rhune, about half way up this 3000 ft. mountain in the Low Pyrenees. The species was not collected. It should be added that it was only on our last day in the high mountains that we discovered the place and conditions most suitable for seeing such migrations.

OBSERVATIONS BY OTHERS IN EUROPE

Our experience at the Port de Gavarnie seems unique, but we presume that this is merely through lack of observation, and that similar movements can be seen in this and other places each year.

Surprisingly, there are scarcely any published records of passerine birds seen migrating through high mountains. There has been heated discussion as to whether birds do or do not cross the Alps, but based on indirect evidence, with the contending parties coming to opposite conclusions (Thomson, 1926). Heilfurth (1934) has, however, seen meadow pipits and swallows (*Hirundo rustica*) passing through the Graubünden Alps in spring, and Masarey & Sutter (1939) have trapped various passerine migrants at Realp in autumn. Clay & Meinertzhagen (1933) saw a passage of redstarts, flycatchers, shrikes and hirundines through the Port de Gavarnie on 21 April 1932, and many swallows and pigeons passing there in the autumn. It may reasonably be suggested that such movements would be seen regularly if ornithologists visited the Alps and Pyrenees in April and October, instead of in the tourist season.

Butterflies have been seen travelling north through the Alps and Pyrenees in spring, but southward flights in autumn have rarely been recorded from the mountains, and are only just coming to be regarded as regular anywhere in Europe (Williams, 1930; Williams, Cockbill, Gibbs & Downes, 1942; Muspratt, 1946).

For *Colias croceus*, for instance, Williams *et al.* (1942) can cite only five southward flights in Europe, a total which our records double. One record, on 10 October 1900, was at Gèdre, in the main Gavarnie valley about 8 miles north of the Port. In this and a similar movement on 14 October 1908, the butterflies moved south up the valley, passed Gavarnie and disappeared towards Spain by the Pouey-Aspé valley (which would bring them to the Port). (Rondou, 1932; Williams, 1935; Muspratt, 1950). The data of Muspratt (1950) on the appearances of *C. croceus* at St Jean de Luz, at the western end of the Pyrenees, provide strong inferential evidence for migration in this region. C. B. Williams (*in litt.*) now writes that records which he is shortly publishing demonstrate

a regular southward movement of *C. croceus* in England in autumn.

For *Vanessa atalanta*, a regular southward flight in autumn has recently been established in England, but outside Britain there are records for only one place in Switzerland and one in Austria (Williams *et al.* 1942). Williams (1930, 1939) tabulates many southward flights of *Pieris brassicae*, chiefly from Central Europe, especially Germany, in late July and August. But for Central and Southern France he lists only one southward flight and other mass appearances, these like our records being in late September. Williams (1930) gives no record of a southward flight of *Pontia daplidice*, but it is a well-known immigrant to Britain.

In summaries prepared by Williams (1929, 1930), the few records for migrating dragonflies contrast with the many for migrating butterflies. Since then, there have been some further records for dragonflies but mainly of mass appearances, not of directional flights in progress. Mass flights of *Sympetrum striolatum* have, however, been seen southward in Italy on 1 November (Fraser, 1945), northward in South Wales on 2 July (Longfield, 1950), and northward in southern Ireland in late August and early September (Longfield, 1948). In south-western France, large numbers of *S. meridionale* were seen moving west on the Gironde between mid-September and mid-October (Dannreuther, 1947), and an unidentified species passed south-west along the cliffs against the wind at Guéthary, near St Jean de Luz, on 9 November (Dannreuther, 1949). There is a record of dragonflies migrating through mountains by Fowler (1891, pp. 202-3), who saw large numbers moving west at Andermatt in Switzerland in late September 1886. The best known dragonfly migrant is *Libellula quadrimaculata*, which moves west in large numbers in northern Europe in May and June, the numbers apparently varying greatly in different years (McLachlan, 1900; Dannreuther, 1941). Dannreuther (1941) also refers to a few other species seen travelling.

We can find no previous records for migration in syrphid flies, in the sense of directed movements independent of the wind, but large swarms have occasionally been seen, as in Essex and Kent in August 1869 (Verrall, 1901, pp. 339-40), in the North Sea on 16 and 23 July 1938 (Dannreuther, 1939), in Essex on 24 July 1945 (Dannreuther, 1946), off Selsey Bill on 11-12 August 1947 (Dannreuther, 1948), and, more remarkably, in North-East Land, Spitsbergen, in early August 1924 (Elton, 1925). The record for 1945 and the first for 1938 refer to *Episyrphus balteatus*, which was also included with other species in the 1869 swarms. (Wainwright (1944) and Goffe (1945) discuss syrphid 'migrations', but only in terms of individuals of rare species crossing the sea to Britain.)

OBSERVATIONS OUTSIDE EUROPE

There appear to be no other records of birds seen migrating through high mountains, though they must do so at times, as various migrants occur, for instance, in Tibet (Kinnear & Wollaston, 1922). Butterflies have been seen migrating through the Himalayas at heights considerably greater than the Pyrenees, and there are also records from African mountains (Williams, 1930; Williams *et al.* 1942). The closest parallel with the present observations is the discovery by Beebe (1947, 1949) of bird and insect migrations at the Portachuelo Pass at 3000 ft. in Venezuela. In the case of the birds, Beebe's observations suggest more a drift through the general region than a concentrated stream through the pass itself, and only one species, the martin *Phaeoprogne tapera*, was seen actually travelling in large numbers. Butterflies, on the other hand, passed in vastly greater numbers than any we saw in the Pyrenees. Apparently the movement is unidirectional, and there is no return flight. Beebe adds that many other orders of insects migrate through the pass, and will be described in later papers.

THE VALUE OF MIGRATION

The significance of migration in birds has long been appreciated. The migrants breed in an area which at some other season is unfavourable, they move out after breeding, and return in the following year. In Europe, the migratory movements are chiefly south and west in autumn and the reverse in spring.

In addition to regular migrants, there are a few species which irrupt irregularly every few years, such as waxwing (*Bombicilla garrulus*), crossbill (*Loxia curvirostra*) and rosy pastor (*Pastor roseus*). Such invasions have usually been attributed to exodus after overpopulation, but this could scarcely be the whole story, as a habit causing the extinction of the individuals possessing it could not persist in the species. In fact, the waxwing has now been proved through ringing to return to its breeding grounds, while crossbill and pastor have been shown to shift their breeding grounds in response to food shortage, and some movement occurs each year. The wandering habit is chiefly of value in normal years, causing the birds to leave unfavourable areas, and thus increasing their chances of finding favourable ones (Lack, 1951*b*). Kalela (1949) has similarly interpreted the well-known movements of the lemming (*Lemmus lemmus*). On this view, the periodic huge, and apparently disastrous, emigrations of crossbill, lemming and others are due to the failure of suitable conditions over a wide area. The disaster is not the emigration, but the situation which gives rise to it. The animals would have perished had they stayed, and emigration (of ad-

vantage in normal years) gives them a chance of finding suitable ground even in a bad year. Crossbill and lemming have sometimes colonized new areas after big irruptions.

Both migration and emigration have been invoked to account for butterfly 'migrations', the lepidopterist using this term in a wider sense than the ornithologist, to cover any long-distance movement. As regards British butterflies, Ford (1945, p. 164) writes that 'the cause of large-scale migrations is quite unknown', and he lists overpopulation, extension of range, and climatic factors as points to be considered, while for one species, the monarch (*Danaus plexippus*) of North America, he adds that a regular, twice-yearly migration, north in spring and south in autumn, has been established. The northward movements of European butterflies in early summer are well known, but southward flights have rarely been seen. Nevertheless, Williams *et al.* (1942) now argue strongly in favour of regular two-way migrations. First, the case of *D. plexippus* shows that such a thing is possible in butterflies. Secondly, if the northward flights were merely due to overpopulation or to vain attempts to extend the range, and were followed by death, the habit would presumably be eliminated. Thirdly, the records of southward flights, though still mainly casual, are increasing. Williams suggests that the apparent rarity of southward flights may be partly due to the scarcity of observers in southern Europe, a suggestion which our observations confirm.

While the migrations of many butterflies now appear to be twice-yearly movements away from and back to the same areas, they differ from those of birds in that breeding usually takes place in both summer and winter habitats, so that it is a different generation which makes each flight. *D. plexippus* is, however, an exception, breeding only in its northern habitat. In addition to such regular migrations, it is of course possible that other butterflies have emigratory movements comparable with those of lemming and crossbill, and correlated with food shortage and overpopulation. But the apparent absence of a return flight, as reported for instance by Beebe (1949), is not by itself sufficient evidence for emigration. The return flight might occur along a different route, as happens in certain birds.

Dragonfly migrations have generally been attributed to emigration following overpopulation (Fraser, 1943, 1945; Longfield, 1948). Fraser (1943), finding the waters swarming with cannibalistic larvae, remarks 'in the fierce struggle engendered by overcrowding . . . the desire to escape from such a hell' etc., though the overcrowding in hell refers to the larvae in the pond, the migration to winged forms already in the heavens. Presumably what is meant is that adult dragonflies have a response to overcrowding similar to that of

crossbill and lemming (also locust), which takes them away from places where breeding would be unfavourable. In support of this, Fraser (1943) claims that migration occurs only in the teneral adults just after emergence, but in a later record of migration many males were fully adult (Fraser, 1945) and this also held for most and perhaps all the individuals which we saw at the Port de Gavarnie. It may therefore be suggested that some dragonflies, notably *Sympetrum*, have twice-yearly, two-way migrations like birds and butterflies. In this connexion it is interesting that the North American species *S. rubicundus* (Jay) and *Anax junius* (Drury) have been reported as flying south or southwest in September and October (Dannreuther, 1941).

In syrphid flies, as already mentioned, there is no previous evidence for directed movements. This does not necessarily mean that they are rare. Most records of butterfly migration come from inexperienced persons, usually not entomologists at all, and other kinds of insects are much less conspicuous than butterflies. If, too, the migrations normally occur on a broad front, it might well need the concentration of a geographical barrier before they became at all obvious to the untrained eye. While, therefore, it would not be permissible to argue from one flight that syrphid flies make regular migrations, this possibility should certainly be kept in mind for the future.

It has recently been shown that migratory birds normally travel on a 'standard direction', from which they can be deflected locally and temporarily by a barrier such as the sea or high ground. Concentrated flights can then be observed along the edge of the barrier. In the region of Gavarnie, for instance, the small passerine birds and pigeons fly south up the long valley from the plains, but near the head they often leave it for a less steep subsidiary valley running south-west, while many of those that continue south up to the Cirque are there deflected west by the huge precipices. Both groups are thus brought eventually to the Port de Gavarnie, where they cross at the lowest point, and so come through the pass in a concentrated stream WSW. It seems very possible that migrating insects follow the same route. Had the insects coming through the Port been travelling WSW. the whole time, there is no reason why they should have been concentrated at this place. Further, *Colias croceus* has twice been seen moving south up the main Gavarnie valley in large numbers from Gèdre, suggesting that this species, at least, may fly up southwards from the plains on a broad front, gradually becoming concentrated by the narrowing steep-sided valley, and eventually being deflected to the WSW. by the mountain barrier. Williams (1949) states that, while migrating butterflies tend to keep to their standard directions, they are sometimes deflected by a coast-line or the windings of a steep valley.

ACKNOWLEDGEMENTS

We are very grateful to Miss M. M. Betts for determining, and to Lt.-Col. F. C. Fraser and Mr E. Taylor for checking, the identification of the dragonflies and syrphids, which have been deposited at the Hope Department, Oxford University. We are also very grateful to Miss C. Longfield, Capt. T. Dannreuther and Dr C. B. Williams for their trouble in helping us with the literature and to R. E. Moreau, Dr C. B. Williams and Prof. G. C. Varley for criticizing the MS. The expenses of the senior author were largely defrayed by a grant from the Royal Society, to whom we are extremely grateful.

SUMMARY

1. In the autumn of 1950, small passerine birds, pigeons, butterflies of several species, one species of dragonfly and one species of syrphid fly were seen migrating south and west through the Pyrenees. The syrphids were particularly abundant.

2. The most spectacular migration occurred (against the wind) through a pass at 7500 ft., and it is suggested that the insects, like the birds, might have been somewhat deflected from their standard flight-direction, and concentrated, by the mountain barriers.

3. Migrations and emigrations in birds are compared with the parallel phenomena in insects.

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AN ECOLOGICAL STUDY OF THE RIVER TOWY

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(With 3 Figures in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	68	4. THE FAUNA	75
2. THE ENVIRONMENT	68	5. THE FOOD OF THE MINNOWS	81
(a) Topography	68	6. THE FOOD OF SOME OF THE CHARACTERISTIC	
(b) The river water	68	INVERTEBRATE ANIMALS OF THE MAINSTREAM	83
(c) The regions examined	70	7. SUMMARY	85
3. THE FLORA	74	REFERENCES	85

1. INTRODUCTION

In papers recently published in this *Journal* the writer (1949*a, b*, 1950) has described the general ecology of two British rivers of different type. One of these is the Rheidol, which flows into Cardigan Bay. Here the general conditions may be described as severe; the river has a very unstable, gravelly bed and is liable to frequent, heavy floods; the water is very soft and acid, its pH swinging from 5·8 to 6·4; the macroflora is somewhat scanty; the fauna, which includes about 130 mainstream species, is characterized rather by number of species than by numbers of individuals; the chief foods of the common phytophagous species are dead leaves, detritus, the 'red' algae *Lemanea* and *Batrachospermum*, the green algae *Stigeoclonium* and *Microspora* and the diatoms. The other is the river Sawdde, a swift, stony trout-stream flowing on the northern side of a range of hills in South Wales. Here the general conditions are favourable; the stream-water is moderately calcareous and alkaline, the river is not liable to severe flooding and its bed is very stable; there is ample bryophyte growth and a rich algal flora; the fauna during the summer includes about 75 species, and the main foods of the common phytophagous insects are detritus, the moss *Fontinalis antipyretica*, diatoms and the green alga *Ulothrix*.

The present paper deals with the general ecology of a third type of river, the Towy, which is a much larger river than the Rheidol or the Sawdde, with soft, nearly neutral water, a comparatively long lowland course and a rich algal and phanerogamic flora. The general plan of the work follows closely that of the earlier study of the Sawdde (Jones, 1949*b*); it includes a qualitative survey of the flora, qualitative and quantitative work on the fauna and observations on the feeding habits of some of the chief animals.

2. THE ENVIRONMENT

(a) *Topography*

The river has its source at an altitude of about 1400 ft. in barren and inaccessible country in the hills of central Wales (Fig. 1). Its valley, for the first 13 miles, is narrow and steep-sided and then begins to open so that at Llandovery its floor is about a quarter of a mile in width. Thereafter the river turns to the southwest and its course gradually becomes more erratic, but it does not begin to meander until it reaches Llandilo, where it turns westwards. At Carmarthen the river becomes tidal, turns southwards and flows into the Bristol Channel. The profile of the mainstream (Fig. 2) is that of a mature, corrading stream; the gradient diminishes more or less steadily from the source of the river to its mouth and there appear to be no weirs or falls to present obstacles to migratory fish.

Except in abnormally wet seasons the river is not liable to frequent floods, is not silted up to any appreciable extent and appears to maintain its course without much artificial banking. There are numerous tributaries and a reasonably good flow is retained even at the end of a long, dry summer such as that of 1949.

(b) *The river water*

The major part of the catchment area has a mean annual rainfall of 50–60 in. Over most of its course the water of the mainstream is nearly neutral in reaction. The results of a series of colorimetric pH determinations made in July 1949 are inserted in Fig. 3; this shows that near its source the river is faintly acid; below Llandovery four important tributaries with alkaline water (pH values 7·4, 7·4, 8·0, 8·0) enter the mainstream from the south and west, but their effect is offset to some extent by

tributaries from the north which add more water which is approximately neutral. The combined effect of all the tributaries is to give the mainstream below Llangadock a faint degree of alkalinity; many pH determinations between Llandilo and Carmarthen gave consistent results of 7.2. No analyses of the river

water were made but there is no reason to expect any abnormal chemical features; there is no industrial pollution of any type nor does there appear to be any harmful degree of sewage pollution, for the only towns of any size along the river are Llandovery and Llandilo, each with a population of about 2000.

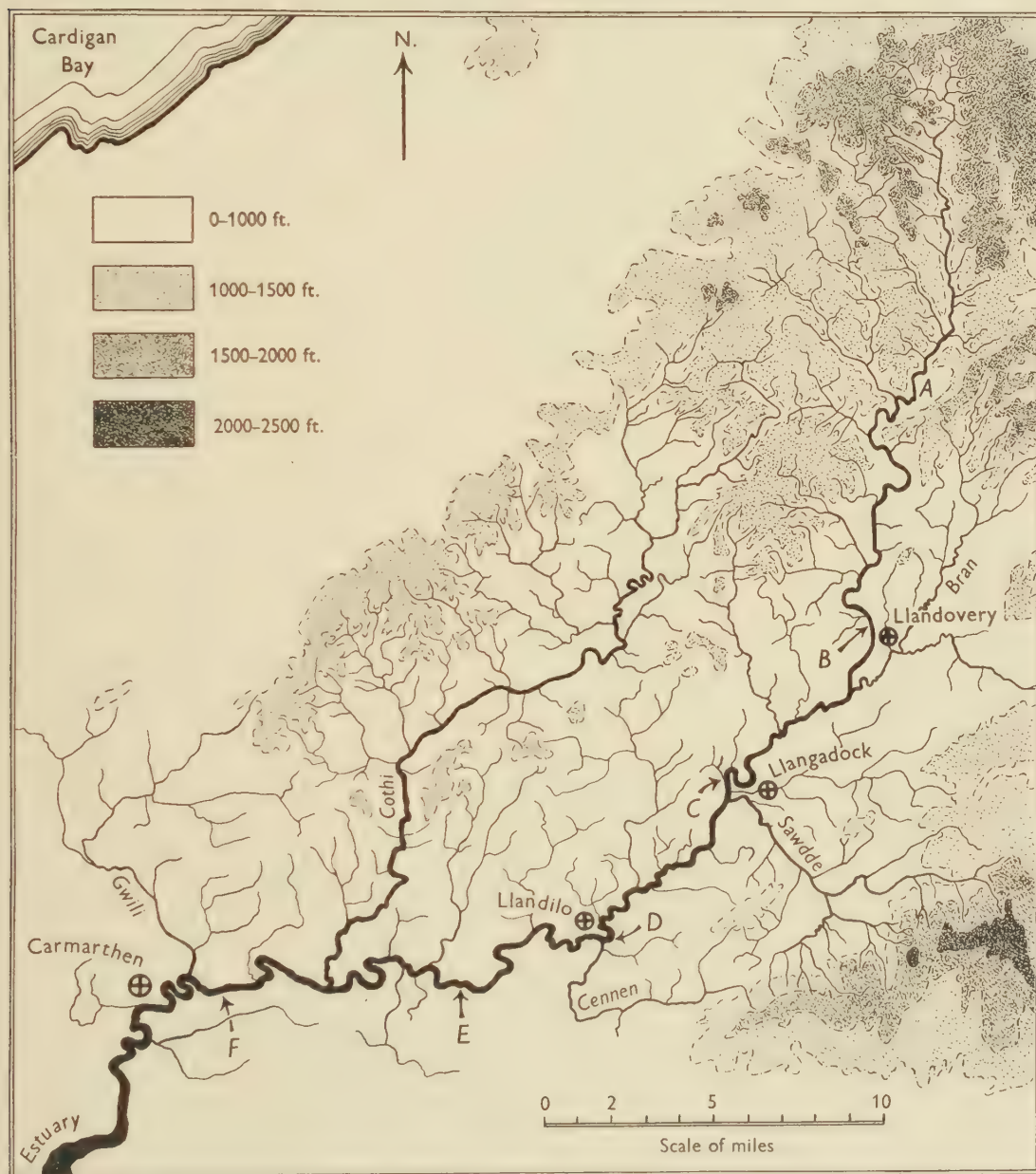


Fig. 1. Map of the River Towy and its tributaries, showing the relief of the land and the position of the collecting stations A-F.

(c) The regions examined

Six representative stations on the mainstream were selected for the examination of the flora and fauna. The highest of these (A) is situated at Ystrad-ffin, about 10 miles above Llandovery. Here the gradient of the river bed is about 60 ft. per mile; the stream flows rather swiftly, is about 70 ft. in width and generally shallow. The river bed is somewhat flat and remarkably stable, formed by large flat, rough stones well interlocked, interspersed with gravel and

average gradient of 8 ft. per mile and has increased in size considerably, being about 100 ft. from bank to bank. There are long, shallow riffles where the bed is flat and very uniform, composed of small stones, pebbles and gravel; here again the stability of the river bed is a conspicuous feature, for stirring it up with the foot demands considerable effort. At other points the river is fairly deep, bottomed by rock covered with great masses of *Fontinalis* and there are limited areas of slack water with sand bottom on

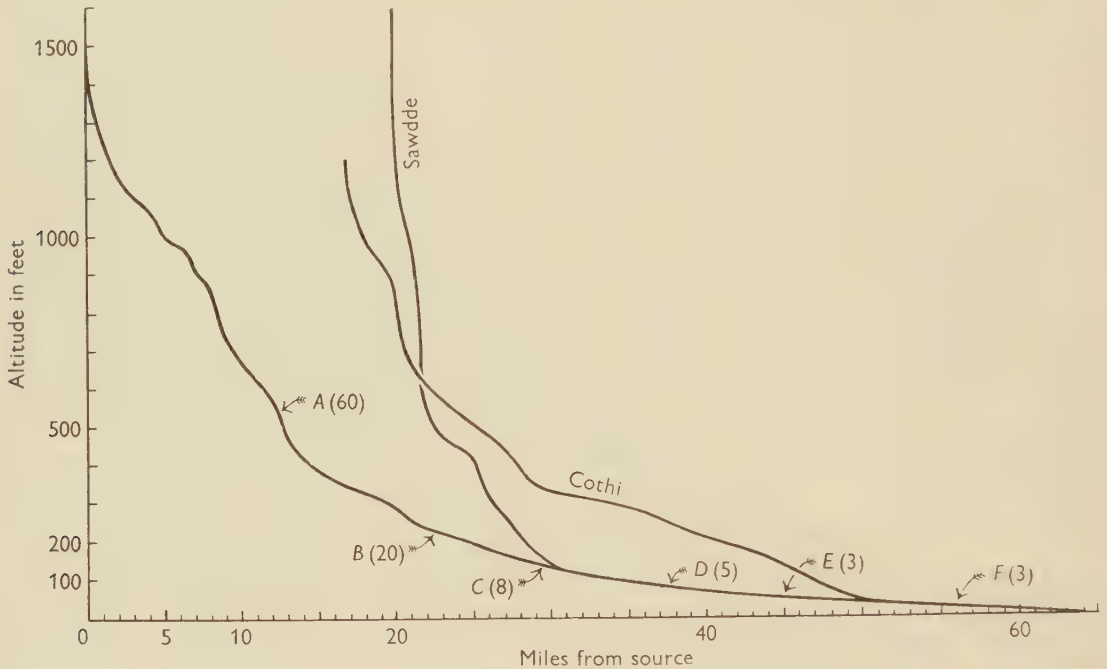


Fig. 2. The profile of the mainstream of the River Towy and its two chief tributaries. A-F, position of collecting stations; bracketed figures are approximate gradients in feet per mile.

small pebbles and supporting a plentiful growth of the moss *Fontinalis antipyretica*. The nature of the bed tends to limit the fauna to animals such as *Ancylastrum*, *Glossosoma* and *Simulium* which live upon the stones, and types which find shelter in the moss. Here and there near the margins large boulders break the current and there are small pools of slack water thick with algal growth, but there are no deposits of sand and no phanerogamic vegetation.

The second station (B) is at Dolau Hirton, 1 mile above Llandovery. Here the river is of very varied nature. The average gradient is about 20 ft. per mile, there are broad shallows of gentle flowing water bottomed with weathered stones and pebbles, rocky, alga-covered rapids over which the water pours very swiftly and rock pools up to 15 ft. in depth. At station C (Llangadock Bridge) the river has an

which there are small clumps of *Myriophyllum*, *Ranunculus* and *Callitriche*. There is a plentiful growth of *Elodea* in pools near by, but this plant does not seem to grow in the mainstream.

Station D is about a quarter of a mile below the suspension bridge at Llandilo. The river is here about 150 ft. wide, for the most part shallow and swift flowing with a flat, uniform and very stable pebble-gravel bed. Near the left bank there are extensive deposits of sand with abundant phanerogamic vegetation, the dominant form being *Ranunculus fluitans*; small clumps of *Fontinalis* are dotted about the stony areas. The gradient is now 5 ft. per mile and the flow of water much greater than at station C. At E, the bridge at Dryslwyn Castle, the gradient has slackened to 3 ft. per mile; near the bridge the river is 150 ft. wide, deep and very slow flowing. Along the

right bank there are extensive deposits of muddy sand with a great bed of *Myriophyllum* about 10 ft. in width and about 300 ft. in length. Some distance below the bridge the river gradually becomes more and more shallow, the *Myriophyllum* becomes replaced by *Ranunculus* and *Callitriche*, and then all phanerogamic vegetation disappears as the stream forms a shallow, pebble- and sand-bottomed riffle sweeping round broad flood-beaches.

Below Dryslwyn the river does not change in character to any marked extent, tending to increase in depth rather than in width as it cuts deeper and deeper into thick, rich soil. The tidal area is reached near Carmarthen and station F is approximately at the highest point to which spring tides ascend. Here, at low level, the river flows between almost vertical banks about 10 ft. in height and is still quite shallow with a pebble and gravel bed of much the same nature

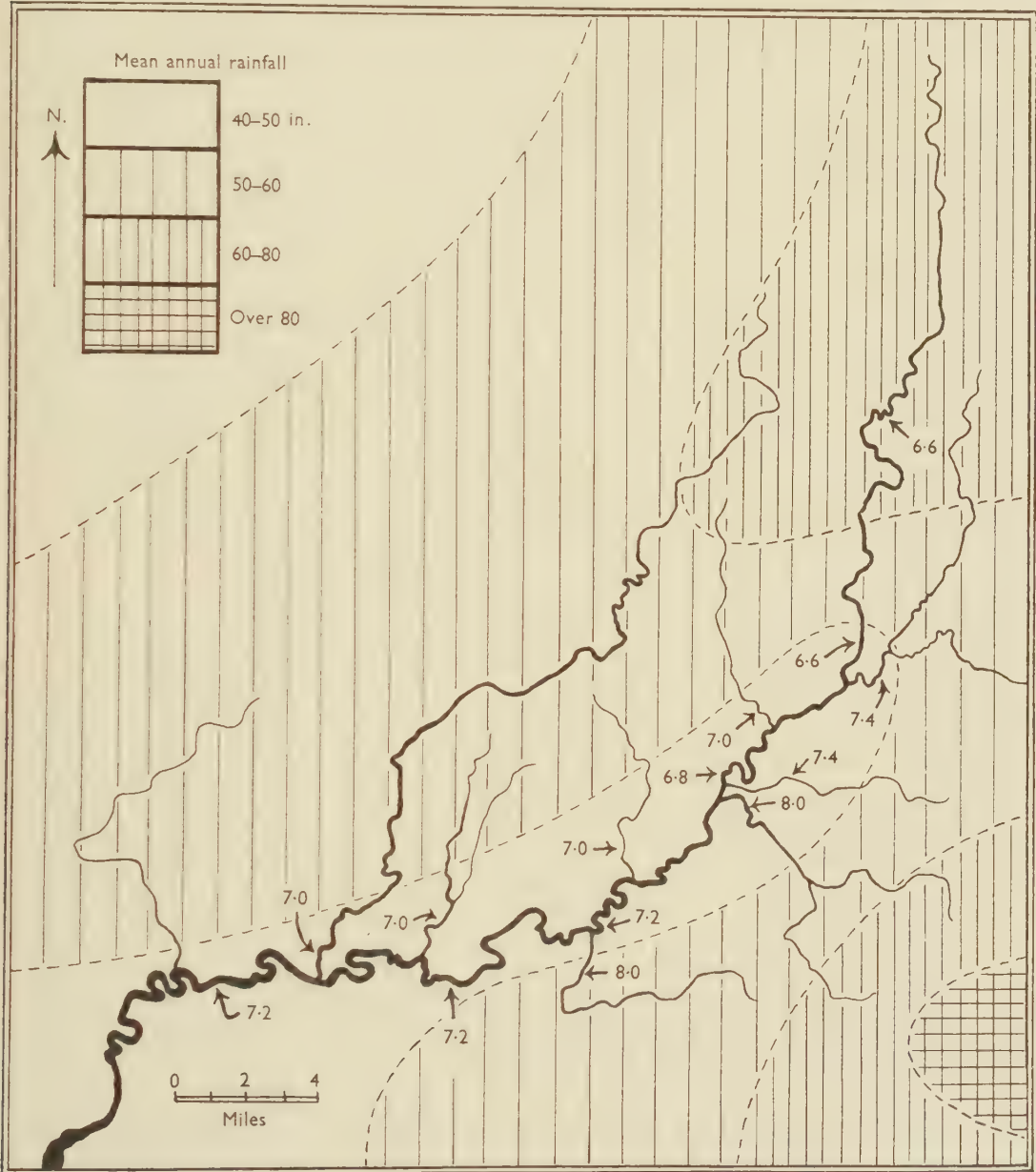


Fig. 3. Sketch map of the river to show the mean annual rainfall and a set of pH records made in July 1949.

An ecological study of the River Towy

Table 1. The flora of the River Towy

(v, very rare; r, rare or infrequent; C, common; A, abundant; as explained in the text.)

Station	A	B	C	D	E	F
Examination dates (1949)	8 July 20 Aug.	8 July 19 July 12 Aug. 30 Aug. 10 Sept.	6 July 28 July 10 Aug. 23 Aug. 3 Sept.	4 July 11 July 8 Aug. 17 Aug. 30 Aug. 24 Sept.	2 July 10 July 25 July 6 Aug. 14 Aug. 7 Sept.	4 July 17 July 14 Aug. 28 Aug. 19 Sept.
PHANEROGAMA						
Ranunculus fluitans Lam.	.	.	r	C	C	C
Callitriche sp.	.	.	r	C	C	C
Myriophyllum sp.	.	.	r	r	A	C
Glyceria fluitans Br.	.	r	C	r	r	r
Potamogeton sp.	.	.	.	.	r	.
BRYOPHYTA						
Fontinalis antipyretica L.	A	C	A	r	.	.
MYXOPHYCEAE						
Merismopedia glauca (Ehr.) Näg.	.	.	.	r	r	v
Coelosphaerium kuetzingianum Näg.	.	.	.	r	C	C
Chamaesiphonales spp.	r	C	A	C	C	r
Phormidium spp.	r	r	r	C	C	C
Oscillatoria sp.	.	.	.	v	r	.
Nostoc sp.	.	.	.	.	.	r
Tolypothrix sp.	C	r	v	.	.	r
CHRYSTOPHYCEAE						
Syncrypta volvox	.	r	.	.	r	.
CHLOROPHYCEAE						
Gonium pectorale Müll.	.	.	v	r	r	r
Pandorina morum Bory	.	.	.	v	r	.
Sphaerocystis Schroeteri Chod.	.	r	r	r	C	C
Apicocystis brauniana Näg.	.	.	.	.	r	r
Ulothrix zonata (Web. & Mohr) Kütz.	.	.	r	v	.	.
Microspora amoena (Kütz.) Rab.	.	v	A	r	r	.
Stigeoclonium sp.	.	r	C	r	r	r
Aphanochaete repens A. Br.	.	.	r	.	.	.
Coleochaete scutata Bréb.	.	.	r	.	.	.
Oedogonium spp.	r	r	A	A	A	A
Bulbochaete sp.	C	r	C	.	v	v
Pediastrum boryanum (Turp.) Menegh.	v	r	r	C	C	C
P. tetras (Ehr.) Ralfs	v	r	r	r	r	r
Coelastrum sphaericum Näg.	.	v	r	r	C	C
C. microporum Näg.	.	.	r	.	.	.
Dictyosphaerium ehrenbergianum Näg.	v	v	r	r	C	C
Ankistrodesmus falcatus (Corda) Ralfs	C	r	r	r	r	C
Selenastrum westii G. M. Smith	r	.	r	r	r	r
Kirchneriella obesa (W. West) Schmidle	.	.	v	r	r	r
Tetraëdron minimum (A. Br.) Hansg.	.	.	.	v	r	r
Scenedesmus obliquus (Turp.) Kütz.	r	A	A	A	A	A
S. bijuga (Turp.) Lagerh.	r	C	r	r	r	r
S. quadricauda (Turp.) Bréb.	.	v	r	r	r	r
S. hystrix Lagerh.	r	r	r	r	r	r
Mougeotia sp.	r	C	r	r	C	C
Zygnema sp.	C	A	v	v	C	C
Spirogyra spp.	v	v	A	A	A	A
Spirotaenia condensata Bréb.	v	r	.	.	.	.
S. obscura Ralfs	v	v	v	.	.	.
Penium margaritaceum (Ehrenb.) Bréb.	.	.	v	.	.	.
Closterium parvulum Näg.	.	.	.	.	r	C
C. leibleinii Kütz.	r	C	C	C	C	C
C. moniliferum (Bory) Ehrenb.	.	r	C	r	r	C
C. ehrenbergii Menegh.	v	r	r	r	r	r
C. acerosum (Schrank) Ehrenb.	.	v	r	r	r	r
C. subulatum (Kütz.) Bréb.	C	r	r	r	r	r
Pleurotaenium trabecula (Ehrenb.) Näg.	.	.	v	v	r	r
Euastrum dubium Näg.	.	r	.	.	.	.
E. verrucosum Ehrenb.	.	.	.	.	v	.
Micrasterias papillifera Bréb.	.	v	v	.	.	.
Cosmarium bioculatum Bréb.	r	r	r	r	r	r
C. humile (Gay) Nordst.	.	r	.	r	r	.
C. subcrenatum Hantzsch.	.	r	r	r	r	r
C. turpinii Bréb.	.	.	.	r	r	r
C. punctulatum Bréb.	.	.	.	r	r	r
C. botrytis Menegh.	.	.	r	r	r	r
C. reniforme (Ralfs) Arch.	.	.	.	v	r	r
Xanthidium antilopaeum (Bréb.) Kütz.	.	.	.	.	r	r
Arthrodesmus convergens Ehrenb.	.	.	.	.	.	r
Staurostrum brevispinum Bréb.	.	.	r	.	.	.
S. orbiculare Ralfs	.	.	r	.	r	r
S. punctulatum Bréb.	r	C	r	v	v	r

Table 1 (cont.)

Station	...	A	B	C	D	E	F
Examination dates (1949)	...	8 July 20 Aug.	8 July 19 July 12 Aug. 30 Aug. 10 Sept.	6 July 28 July 10 Aug. 23 Aug. 3 Sept.	4 July 11 July 8 Aug. 17 Aug. 30 Aug. 24 Sept.	2 July 10 July 25 July 6 Aug. 14 Aug. 7 Sept.	4 July 17 July 14 Aug. 28 Aug. 19 Sept.
CHLOROPHYCEAE (cont.)							
<i>S. dickiei</i> Ralfs		C	C	C	r	r	r
<i>S. dickiei</i> var. <i>circulare</i> Turn.		.	.	.	r	.	.
<i>S. dejectum</i> Bréb.		.	.	.	.	.	.
<i>S. dejectum</i> var. <i>patens</i> Nordst. }	r	r	r	C	C	C	C
<i>S. cuspidatum</i> Bréb.	.	.	.	v	.	.	v
<i>S. avicula</i> Bréb.	.	.	.	C	C	C	C
<i>S. lunatum</i> Ralfs	.	.	.	.	.	.	v
<i>S. polytrichum</i> Perty	v	r	C	C	C	C	C
<i>S. hirsutum</i> (Ehrenb.) Bréb.	.	.	.	r	.	.	r
<i>S. pilosellum</i> (Näg.) Arch.	.	.	r	r	r	r	r
<i>S. polymorphum</i> Bréb.	.	.	C	C	r	r	r
<i>S. furcatum</i> (Ehrenb.) Bréb.	.	v	.	.	.	.	r
<i>S. furcigerum</i> Bréb.	.	.	v	.	.	.	v
<i>Cosmocladium saxonicum</i> De Bary	.	.	.	.	.	.	r
<i>Sphaerozosma vertebratum</i> (Bréb.) Ralfs	r	.	.	.	.	.	.
<i>Spondylosium papillosum</i> W. & G. S. West	C	.	r	r	r	r	r
<i>Hyalotheca dissiliens</i> (Sm.) Bréb.	r	C	r	r	r	r	r
<i>Desmidium swartzii</i> Ag.	.	.	.	.	.	v	r
BACILLARIAE							
<i>Melosira varians</i> Ag.	.	.	r	C	C	C	C
<i>Cyclotella</i> sp.	.	.	v	r	r	r	r
<i>Tabellaria flocculosa</i> (Roth.) Kütz.	C	C	A	C	r	r	r
<i>Meridion circulare</i> Ag.	v	r	C	r	r	v	v
<i>Diatoma vulgare</i> Bory	.	.	v	r	C	A	A
<i>D. hiemale</i> var. <i>mesodon</i> (Ehr.) Grun.	r	r	v	.	v	.	.
<i>Fragilaria crotonensis</i> Kitton	r	C	A	A	A	A	A
<i>F. capucina</i> Desmaz.	.	.	v	v	r	v	v
<i>Synedra ulna</i> (Nitzsch.) Ehr.	v	r	C	C	C	C	C
<i>S. pulchella</i> Kütz.	.	.	r	r	C	C	C
<i>Eunotia lunaris</i> (Ehr.) Grun.	r	v	r	.	.	.	.
<i>E. sudetica</i> (O. Müll.) Hist.	.	r	.	.	.	.	.
<i>Ceratoneis arcus</i> Kütz.	C	C	C	C	r	r	r
<i>Achnanthes microcephala</i> Kütz.	.	r	C	v	v	C	C
<i>A. minutissima</i> var. <i>cryptocephala</i> Grun. }	A	A	A	C	C	C	C
<i>A. linearis</i> W. Smith	.	.	.	v	v	.	.
<i>A. lanceolata</i> Bréb.	.	r	.	r	r	r	r
<i>Cocconeis placentula</i> Ehr.	.	r	r	r	r	r	r
<i>C. pediculus</i> Ehr.	.	.	.	v	r	.	.
<i>Navicula viridula</i> Kütz.	v	v	r	r	r	r	r
<i>N. radiosa</i> Kütz.	C	r	v	v	v	v	v
<i>N. rhynchocephala</i> Kütz.	.	v	v	v	r	v	v
<i>N. cryptocephala</i> Kütz.	.	r	C	C	C	C	C
<i>N. rotacana</i> (Rabh.) Grun.	v	v	r	r	v	.	.
<i>Pinnularia viridis</i> (Nitzsch.) Ehr.	.	v	v	v	.	.	.
<i>P. maior</i> (Kütz.) Cleve	.	v	r	.	v	.	.
<i>P. interrupta</i> W. Smith	v	v	.	.	.	.	.
<i>P. divergens</i> W. Smith	v	v	.	.	.	.	.
<i>P. borealis</i> Ehr.	.	.	v	v	.	.	.
<i>P. gibba</i> Ehr.	.	.	r	.	.	.	.
<i>Caloneis amphisbaena</i> (Bory) Cleve	.	.	.	r	.	.	.
<i>C. silicula</i> (Ehr.) Cleve	.	v	.	.	.	.	.
<i>Neidium affine</i> (Ehr.) Cleve	.	.	.	r	r	r	r
<i>Stauroneis phoenicenteron</i> Ehr.	.	.	v	v	r	r	r
<i>Frustulia rhomboides</i> (Ehr.) de Toni	C	r	v	v	r	.	.
<i>F. vulgaris</i> Thwaites	v	v	v	v	v	.	.
<i>Gomphonema acuminatum</i> Ehr.	v	v	v	v	v	r	r
<i>G. parvulum</i> (Kütz.) Grun.	C	r	r	r	r	r	r
<i>G. constrictum</i> Ehr.	.	v	C	C	C	C	C
<i>G. olivaceum</i> (Lyngb.) Kütz.	.	.	v	.	.	.	.
<i>G. angustatum</i> (Kütz.) Rabh.	v	v	v	v	v	v	v
<i>Cymbella cuspidata</i> Kütz.	.	.	r	r	r	r	r
<i>C. ventricosa</i> Kütz.	C	C	C	C	C	C	C
<i>C. sinuata</i> Greg.	.	.	.	v	r	r	r
<i>C. affinis</i> Kütz.	.	.	.	v	C	v	v
<i>C. helvetica</i> Kütz.	.	.	.	v	v	.	.
<i>Amphora ovalis</i> Kütz.	.	.	r	r	r	r	r
<i>Nitzschia palea</i> (Kütz.) W. Smith	v	r	C	C	C	r	r
<i>N. vivax</i> W. Smith	.	.	r	.	.	.	.
<i>N. linearis</i> W. Smith	.	.	.	v	.	r	r
<i>N. acicularis</i> W. Smith	.	.	.	r	r	r	r
<i>N. dissipata</i> (Kütz.) Grun.	.	.	.	.	r	.	.
<i>Surirella</i> spp.	v	r	r	r	r	.	.
<i>Cymatopleura solea</i> (Bréb.) W. Smith	.	.	.	v	r	r	r

as that at Llandilo and Llangadock. Near the banks there are deposits of sand and a fair amount of phanerogamic vegetation. The most striking feature of this locality in the summer of 1949 was the richness of the algal growth on the stream-bed, most of which was usually covered with a thick, green-brown, woolly mass, mainly composed of *Oedogonium*, *Spirogyra*, *Scenedesmus*, *Diatoma* and *Fragilaria*. In flood the level of the water may rise 6–7 ft. and the river will have a discharge which may be very roughly estimated at about 150,000 cu.ft per min.

3. THE FLORA

A qualitative study of the flora was made in the summer of 1949, on the dates set out at the head of Table 1, which records all the plants seen in the mainstream of the river; no backwaters or cut-offs were investigated. On each date notes were made on the distribution of phanerogams, bryophytes and filamentous algae and material for examination was collected from stones, rocks and submerged macrophytes. It was not always possible to identify the filamentous algae in the field, and for checking their distribution a very simple expedient was found useful; specimen tubes of three sizes were carried, samples of algae which appeared abundant and widespread were placed in the largest tubes, samples of less common types in tubes of medium size and the smallest used for what appeared to be rare. In Table 1 the plants are roughly classified in four orders of abundance; those seen in every examination of the region specified and evidently dominant types are denoted as abundant; plants of regular occurrence present in moderate numbers or quantity are classified as common. In the case of the desmids, diatoms and other algae seen only with the microscope, a species would be noted as common if, on examining a fresh preparation made in the usual way, one or more individuals would appear in any $\frac{2}{3}$ in. objective field taken at random; with the writer's microscope this would be a field of radius about 600 μ . Microscopic algae seen after some search are denoted as rare or very rare. As far as possible records of diatoms are based on the examination of fresh material, but to check identifications permanent slides were made by 'cleaning' them in the usual way and mounting with Gurr's Clearax. The nomenclature of the diatoms follows Hustedt (1930), that of desmids follows the monograph of West, West & Carter (1904–23), the other algae are named as in Smith (1933).

The distribution of the filamentous green algae appeared to be determined mainly by the force of the current; *Spirogyra* occurred generally where the water was motionless or very slow-moving, pools under bridges appearing to be a favourite locality.

Oedogonium occurred in great abundance where the water was moving fairly slowly and 1–2 ft. deep. *Microspora* and *Stigeoclonium* were characteristic of swift water with a pebble bed, while *Zygnema* appeared in great quantity on the steeply sloping rock bed at station B; the last also turned up in fair quantity at stations E and F but here was mixed with other filamentous algae. Most of the commoner microscopic algae seemed to be quite ubiquitous and on most occasions samples collected from the stream-bed would not be greatly different from 'squeezeings' from the submerged macrophytes, though some of the diatoms, *Achnanthes* and *Diatoma* for example, tended to be more numerous on the stones, while the ribbons of *Fragilaria* and certain stalked forms like *Gomphonema constrictum* appeared in greatest abundance among the *Myriophyllum* leaves. Most of the green algae occurred throughout the summer, which in 1949 was very dry and sunny. *Scenedesmus obliquus* was most abundant in July; the desmid flora, on the other hand, became much more varied as the summer advanced and a number of the rarer species were first recorded in the middle of August.

Generally speaking the flora is rich; it includes about 130 species of algae, much the same number as that recorded for the non-tidal reaches of the Tees by Butcher, Longwell & Pentelow (1937, pp. 118–21). The flora of the Towy includes fewer diatoms and some of the most abundant and characteristic species of the Tees (*Cocconeis placentula*, *Navicula viridula*, *Cymbella sinuata* and *Gomphonema olivaceum*) are rare or very rare. On the other hand, the Towy flora appears richer in green algae, particularly desmids, for of this group 41 species are recorded whereas the Tees has 7, of which only one (*Closterium leibleinii*) is common. One of the dominant algae of the Tees is *Cladophora glomerata* L. which from time to time was seen to appear in extraordinary profusion, but this alga does not seem to occur in the Towy though it is fairly common in its tributary, the Sawdde.

The microflora of some other British rivers, including the Hull, Itchen, Test, Trent and Tame has been described by Butcher (1940, 1946, 1947), but a detailed comparison of his records with mine would be beyond the scope of this investigation, for my collecting did not include quantitative work and was undertaken mainly to ascertain the range and general nature of the plant food supply available for the animal population.

The spring of 1950 was moderately dry, and when examination of the river was resumed at the end of June the river was at normal level, with an abundant algal flora very similar to that seen in July 1949. The summer that followed, however, was abnormally cool and wet; on 17 August the river rose to a level about 3 ft. above normal at station C and persistent flooding occurred until the end of September (see Fig. 4 and

further information in the following section dealing with the fauna). As a result, the flora which was seen in August and September was markedly different from that recorded for the dry and sunny previous summer. The *Scenedesmus* and many other microscopic green algae disappeared or became very rare, and the masses of *Spirogyra* and *Oedogonium* characteristic of the 1949 season did not develop. At most parts of the river a fairly abundant, though patchy, algal growth persisted; generally the dominant forms were the green algae *Stigeoclonium* and *Ulothrix*. From time to time a heavy diatom growth developed in the river; qualitatively this was very similar to that seen in the previous year, but *Ceratoneis arcus*, a diatom partial to cold waters and usually abundant in spring, was one of the dominant forms.

Stigeoclonium is one of the dominant algae of the river Rheidol (Reese, 1937; Jones 1950); the short, closely bunched filaments of this alga and its very firmly attached prostrate system would seem to make it well adapted for the stony bed of swift, frequently flooding rivers. Butcher *et al.* (1937, p. 118) found it to be an abundant summer form in the Tees, and Butcher (1947, pp. 188-9) has discussed the distribution of the various species of the genus in the rivers Tame and Trent.

4. THE FAUNA

During July and August 1949 a qualitative examination of the fauna of the mainstream was carried out. There was very little rainfall during this period, the level of the river remained rather low and most of its bed could be reached by wading. Nearly all the species recorded were captured with the hand net, but a light dredge and a small bolting cloth bottle-ended net were also employed and sieves used to examine the muddy sand, mainly at station E. Collections from different types of habitat were kept separate. All the animals found are listed in Table 2 with their apparent degree of abundance; v (very rare) denotes that a single specimen only was captured at the collecting station; r, animals of which the total number captured was 2-10; the commoner species are denoted as C (common), N (numerous) and A (abundant). 'Common' species are those which turned up regularly, total number about 10-100; 'numerous' species are those of which about 100-200 occurred in the samples. Information about the 'abundant' animals is given below. One September fauna sample was taken at station B; at stations C-F the very heavy algal growth which developed by the end of August made the collecting of satisfactory September samples impossible. Region A was only visited twice and further examination of the fauna should have been made, but travelling difficulties did not permit of more collecting.

The most characteristic species of the river's summer fauna in 1949 were the minnow, the mayfly, *Ephemera notata*, the caddisfly, *Glossosoma boltoni*, the stonefly, *Leuctra fusciventris*, and the case-building Tanytarsus, a chironomid larva whose very curious Hydra-like case is figured by Butcher *et al.* (1937, p. 150) and by Berg (1948, p. 166). This larva also occurs in the river Liffey (Humphries & Frost, 1937), and is usually referred to the genus or subgenus *Rheotanytarsus*. Other species abundant or numerous, but more restricted in distribution, were the snail, *Hydrobia jenkinsi*, mainly at stations E and F; the estuarine amphipod, *Gammarus zaddachi*, at F; species of the water mites, *Atractides*; the water bug, *Corixa striata*, in the *Myriophyllum* beds at E; the beetle, *Esolus parallelipipedus*, at C; the carnivorous larva of a tipulid fly *Hexatoma*, and of blackflies, *Simulium reptans*.

As the summer of 1949 progressed some changes took place in the fauna. The *Ephemera* nymphs gradually disappeared as they bred out to adults, and most of the *Glossosoma* larvae had turned into pupae by the end of July. In August a great multitude of young *Hydrobia* appeared at stations E and F, crawling about on vegetation growing in slowly flowing water, but the most striking feature of the fauna was the extraordinary abundance of the cases of the *Rheotanytarsus* larvae. Towards the end of the month their cases had been made in such numbers that any stone picked out of shallow, flowing water at D and E would bear dozens or hundreds of them and at some points in region E they formed dense masses a foot or more across, looking like great clumps of moss. It would appear that the larvae are continually making new cases, that a high proportion of the larvae are eaten by fish or predatory insects or that there are many overlapping broods during the summer, for at any one time only a small proportion of the cases appear to be tenanted by larvae and pupae. Towards the end of September the masses of cases were breaking up and floating downstream.

The river provides excellent fishing for brown trout and salmon, and is said to be particularly good for sewin. The water bailiffs state that pike are occasionally taken and that flounders have been caught as far upstream as Llangadock (C) but there seems to be no record of the roach (*Rutilus rutilus*).

At stations C, D, E and F the pebble bed of the more shallow parts of the river is of very uniform nature and lends itself well to quantitative sampling, which was begun in July 1950. The apparatus used was a Surber type sampler (Welch, 1948, p. 321), the base frame, made of heavy strip iron, measured 23.7 × 21 cm. and thus had an area of approximately 500 sq.cm., it was fitted with thin sheet-iron sides 23 cm. long and 15 cm. high and the net mouth was square with 21 cm. sides. The net was made of strong

Table 2. *The fauna of the river Towy; species recorded in the qualitative survey made in the summer of 1949*

v, very rare; r, rare; C, common; N, numerous; A, abundant; as explained in the text.
Habitats are given in the last column according to the following index. Where more than one figure is given the first indicates the favourite habitat and the others refer to situations where the species is less commonly found.

1. Large stones in swiftly flowing water.
2. Stones and pebbles in moderately swift water.
3. Stones, pebbles, gravel and sand in slack water, sometimes with heavy algal growth.
4. Sand-mud-debris bottom of quiet pools of the mainstream.
5. Sand-mud bed mostly covered with *Ranunculus*, *Myriophyllum* and other phanerogamic vegetation.
6. Moss on rock bed.
7. Among the leaves of phanerogams growing in the flowing water.
8. Among the stems of emergent vegetation near the banks.
9. Surface of gently flowing water.
10. Surface of rock pools separated from the mainstream at low level.

Station	...	A	B	C	D	E	F	Habitat
Collecting dates (1949)	...	8 July 20 Aug.	8 July 19 July 12 Aug. 30 Aug. 10 Sept.	6 July 11 July 28 July 23 Aug.	5 July 12 July 10 Aug. 17 Aug.	2 July 10 July 25 July 6 Aug. 25 Aug.	4 July 17 July 14 Aug. 28 Aug.	
HYDROZOA								
<i>Hydra viridissima</i> Pall.	.	.	r	.	.	.	.	6
PLATYHELMIA								
<i>Polycelis cornuta</i> (Johnson)	.	.	r	.	.	r	C	7, 2
<i>Planaria alpina</i> (Dana)	v	v	v	.	.	.	.	2
NEMATHELMINTHES								
<i>Mermis</i> sp.	.	.	.	.	.	.	v	2
OLIGOCHAETA								
<i>Chaetogaster</i> sp.	.	.	.	.	.	.	r	7, 4
<i>Stylaria lacustris</i> L.	.	.	.	r	.	C	r	7
<i>Lumbriculus variegatus</i> Müll.	.	.	.	.	.	r	r	3, 4
Spp. not identified	r	r	r	r	r	r	r	2, 3
HIRUDINEA								
<i>Herpobdella octoculata</i> (L.)	.	.	.	.	.	.	v	3
MOLLUSCA								
<i>Hydrobia jenkinsi</i> Smith	.	.	.	r	.	A	A	7, 3
<i>Limnaea pereger</i> (Müll.)	.	.	v	N	.	N	N	7, 3
<i>Ancylastrum fluviatile</i> (Müll.)	N	C	C	r	.	v	v	2
<i>Pisidium</i> spp.	.	.	.	r	.	r	r	5
CRUSTACEA								
<i>Simocephalus vetulus</i> (O. F. Müller)	.	.	.	C	.	r	N	7, 8
<i>Acroperus harpae</i> Baird	.	.	.	r	.	.	.	8, 7
<i>Alona affinis</i> (Leydig)	.	.	.	r	.	r	N	8, 7
<i>Chydorus sphaericus</i> (O. F. Müller)	.	r	C	N	.	r	C	8, 7
<i>Cyclops fuscus</i> Jurine	.	.	.	.	.	.	.	7, 8
<i>C. macruiroides</i> s. str. Lilljeborg	.	.	C	C	.	r	.	7, 8
<i>Cyclops</i> spp. larvae	.	.	.	.	.	r	.	7, 8
<i>Gammarus pulex</i> (L.)	.	.	.	r	.	.	.	7
<i>G. zaddachi</i> Sexton	.	.	.	.	.	.	A	2, 3, 7
HYDRACARINA								
<i>Sperchon glandulosus</i> Koen.	.	.	v	v	.	.	.	2
<i>S. brevisrostris</i> Koen.	.	r	.	.	.	.	v	2
<i>S. papillosus</i> Sig. Thor	r	.	.	.	.	.	.	2
<i>Diplodontus despiciens</i> (Müll.)	r	r	C	r	.	r	.	2, 3
<i>Limnesia koenikei</i> Piers.	.	.	.	.	.	r	.	7
<i>Lebertia</i> spp.	r	C	C	C	.	N	C	5, 2, 4
<i>Atractides amplexus</i> Koen. }	.	.	.	.	.	.	.	.
<i>A. brevisrostris</i> Halb. }	r	N	C	C	.	C	r	2, 3
<i>Hygrobates naicus</i> (Johnst.)	r	N	r	r	.	r	r	2, 3
<i>Megapus spinipes</i> (C. L. Koch)	r	r	r	r	.	r	.	3
<i>Aturus scaber</i> Kram.	.	.	.	.	.	v	v	2
<i>Mideopsis orbicularis</i> (Müll.)	.	.	.	.	.	v	r	7
*PLECOPTERA								
<i>Perlodes mortoni</i> (Klap.)	r	r	.	.	.	.	.	1
<i>Dinocras cephalotes</i> (Curt.)	.	.	v	v	.	.	.	1
<i>Perla carlukiana</i> Klap.	.	v	r	r	.	r	.	1, 2
<i>Leuctra geniculata</i> Steph.	.	.	C	.	.	r	r	2, 3
<i>L. fusciventris</i> Steph.	C	C	N	N	.	N	r	2, 3
<i>Protonemura meyeri</i> (Pict.)	N	r	.	.	.	.	.	2
EPHEMEROPTERA								
<i>Ecdyonurus venosus</i> (Fab.)	C	C	C	C	.	r	r	2
<i>Ephemerella notata</i> Eaton	r	C	N	N	.	N	C	2, 3, 7
<i>Baetis rhodani</i> (Pict.)	C	C	C	C	.	r	r	2, 7
<i>Caenis</i> sp.	.	.	v	r	.	v	v	5
<i>Chloeon</i> sp.	.	.	.	.	.	C	r	7
ODONATA								
<i>Ischnura elegans</i> (van der Linden)	.	.	.	.	.	r	.	7
<i>Agria virgo</i> (L.)	.	.	.	.	.	.	v	7

Table 2 (cont.)

Station							Habitat
Collecting dates (1949)	A	B	C	D	E	F	
	... 8 July 20 Aug.	8 July 19 July 12 Aug. 30 Aug. 10 Sept.	6 July 11 July 28 July 23 Aug.	5 July 12 July 10 Aug. 17 Aug.	2 July 10 July 25 July 6 Aug. 25 Aug.	4 July 17 July 14 Aug. 28 Aug.	
ODONATA (cont.)							
<i>Cordulegaster boltonii</i> (Donov.)	.	v	.	.	.	.	3
<i>Gomphus vulgatissimus</i> (L.)	.	.	.	.	v	.	7
HEMIPTERA							
<i>Gerris najas</i> (Degeer)	r	N	r	r	r	r	9
<i>G. lacustris</i> (L.)	.	.	.	v	r	r	9
<i>G. gibbifer</i> Schum.	.	C	.	.	.	.	10
<i>Velia currens</i> (Fab.)	r	r	r	.	.	.	9, 8
<i>Aphelocheirus montandoni</i> Horváth	.	.	.	C	C	C	3, 7, 2
<i>Notonecta glauca</i> L.	.	.	.	.	r	r	7
<i>Plea leachi</i> MacG. & Kirk.	.	.	.	.	r	v	7
<i>Corixa falleni</i> (Fieb.)	.	.	.	.	r	.	7
<i>C. striata</i> (L.)	.	v	r	C	A	N	7
<i>Micronecta poweri</i> (D. & S.)	r	r	C	r	N	r	7, 5, 6, 3
TRICHOPTERA							
<i>Sericostoma personatum</i> Spence	v	v	v	v	.	.	3
<i>Leptocerus aterrimus</i> Steph.	.	v	C	r	r	r	2
<i>Plectrocnemia conspersa</i> (Curt.)	C	C	.	.	.	.	3
<i>Philopotamus montanus</i> (Donov.)	r	r	.	.	.	.	2
<i>Rhyacophila</i> sp.	r	r	r	v	.	.	2
<i>Glossosoma boltoni</i> Curt.	C	N	N	N	N	N	2
<i>Hydroptila</i> sp.	.	C	r	v	v	C	3, 4
COLEOPTERA (imagines)							
<i>Brychius elevatus</i> (Panz.)	.	v	C	r	v	v	7, 2
<i>Laccophilus hyalinus</i> (Degeer)	.	.	.	.	r	.	7
<i>Deronectes elegans</i> (Panz.)	.	.	r	C	C	N	6, 7
<i>D. duodecimpustulatus</i> (Fab.)	.	.	r	v	.	.	6
<i>Oreodytes rivalis</i> (Gyll.)	.	r	r	.	.	.	2, 3
<i>O. septentrionalis</i> (Gyll.)	r	C	r	r	r	C	3, 2
<i>Illybius fuliginosus</i> (Fab.)	.	.	v	.	.	.	6
<i>Hydraena gracilis</i> Germar	r	.	.	v	.	.	2
<i>Limnebius truncatellus</i> (Thunb.)	.	r	.	.	.	.	6, 10
<i>Helophorus brevipalpis</i> (Bedel)	.	r	.	.	.	.	10, 8
<i>Elmis maugei</i> Bedel	C	r	r	r	r	v	2, 3
<i>Esolus parallelopipedus</i> (P. W. J. Muller)	r	r	N	C	C	C	2, 3
<i>Limnius tuberculatus</i> (P. W. J. Muller)	C	r	r	r	r	r	2, 3
<i>Latelmis volckmari</i> (Panz.)	r	r	C	C	C	C	3, 7
COLEOPTERA (larvae)							
Dytiscidae	v	r	r	C	C	C	7, 2
Gyrinidae	v	.	.	.	.	.	3
Dryops sp.	r	r	r	.	r	.	2, 3
<i>Elmis maugei</i> Bedel	C	r	v	v	v	v	2
Other Elminae	r	r	C	C	C	C	3, 2, 7
DIPTERA							
<i>Hexatoma</i> sp.	.	r	N	C	C	C	2, 3
<i>Dicranota</i> sp.	r	.	.	.	.	.	2, 3
<i>Pericoma</i> sp.	v	v	.	.	.	.	3
<i>Atherix</i> sp.	v	r	r	r	r	r	3
<i>Pentaneura</i> sp.	r	r	r	r	r	r	2, 3, 7
<i>Anatopynia</i> sp.	r	C	r	r	r	.	3, 5
<i>Prodiamesa olivacea</i> (Meig.)	.	v	C	r	r	.	3, 5, 4
<i>Cricotopus</i> sp.	.	.	.	r	r	N	3, 5
<i>Orthocladiinae</i> spp.	r	C	C	C	C	C	2, 3
<i>Chironomus</i>							
s.g. <i>Chironomus</i> sp.	.	.	C	r	C	r	5, 3
s.g. <i>Endochironomus</i> sp.	.	.	r	r	C	.	5, 3
<i>Tanytarsus</i> sp.	r	r	.	.	r	r	3
<i>Tanytarsus</i> sp. (Rheotanytarsus type)	r	N	A	A	A	A	2, 3, 1
Ceratopogonidae	.	v	.	.	.	r	5, 4
<i>Simulium reptans</i> (L.)	A	N	C	C	r	.	1, 2
<i>S. latipes</i> (Meig.)	r	.	.	.	.	.	1, 2
VERTEBRATA							
<i>Phoxinus phoxinus</i> (L.) (minnow)	C	C	A	A	A	A	7, 6 etc.
<i>Gasterosteus aculeatus</i> L. (3-spined stickleback)	.	.	C	.	.	r	7, 6
<i>Cottus gobio</i> L. (bullhead)	.	.	C	C	r	r	7, 3
<i>Nemacheilus barbatula</i> (L.) (loach)	.	.	C	C	r	r	7, 6
<i>Anguilla anguilla</i> (L.) (eel)	.	.	r	r	C	C	3 etc.
<i>Salmo trutta</i> L. (brown and sea trout)							
<i>Salmo salar</i> L. (salmon)							
<i>Esox lucius</i> L. (pike)							
<i>Platichthys flesus</i> (L.) (flounder)							

See text

* All names of insects are according to the check-list of Kloet & Hincks (1945).

material with about 20 meshes per cm. In use the sampler was placed on the river bed and some stones piled up against each side to prevent it from moving. Each stone enclosed by the base-frame was lifted, placed in the mouth of the net and rubbed clean so that the organisms upon it were carried into the net by the current. When all the stones had been treated in this way and cast aside the small pebbles and gravel remaining within the frame were thoroughly stirred up to dislodge and capture any animals remaining, and the contents of the net were then transferred to the collecting jar. On each occasion the sampler was used five times in flowing water very roughly 4, 6, 8, 10 and 12 in. deep so that the total area of the river bed covered by each collection was approximately 2500 sq.cm. The frame was not placed where clumps of moss or other macrophytes were growing on the stream bed, but apart from this the selection of suitable spots was governed only by the depth of the water. The contents of the collecting jar was examined as soon as possible and all the animals seen with the naked eye were picked out and counted. In some cases the use of sieves was necessary to separate the smaller organisms from the sand and vegetable debris that entered the net. On an average the examination of a sample would take about 2 hr.

During the period covered by the quantitative

at station C, when the river was at normal level or a little below normal, indicated total populations of 613 and 1091 per 2500 sq.cm., *Baetis*, *Ephemerella* and the *Hydracarina* being the most abundant animals. The 10 July collection contained a large number of very small *Baetis* nymphs, otherwise it agreed very well with the sample for 5 July. That taken on 20 July (at depths of 4-12 in.) partly covered what was previously a dry pebble flood beach, for the river had now risen about 6 in., and showed a much lower population, but with *Baetis* again the most numerous animal. Further rainfall occurred in the next 3 days and on 24 July the river had risen about a foot above normal; the sample for this date was therefore taken entirely from newly covered flood beach; this had a fairly heavy growth of *Ulothrix* which had speedily developed. The *Ephemerella* nymphs were the dominant animals in this collection, they appeared to have quickly colonized the newly covered bed and examination of the gut contents of about 20 specimens showed that they were feeding almost exclusively on the fresh growth of *Ulothrix*.

On 29 July the river level had returned to normal, and it was possible to take a sample from the part of the stream-bed investigated on 5 and 10 July. A population of 445 per 2500 sq.cm. was recorded

Table 3. Mainstream water level data for the River Towy at Llangadock bridge (station C); July-September 1950

The figures give the approximate level of the mainstream in feet above (+) or below (-) normal.

July		Aug.		Sept.	
2	+ $\frac{1}{2}$	5	0	1	+1
5	0	12	+1	5	+1
7	0	17	+3	7	+3
10	- $\frac{1}{4}$	20	+3	8	+2 $\frac{1}{2}$
15	0	25	+1 $\frac{3}{4}$	10	+1
20	+ $\frac{1}{2}$	29	+2	13	+1 $\frac{3}{4}$
24	+1			15	+1 $\frac{1}{2}$
27	+1			17	+3 $\frac{1}{4}$
29	0			19	+2
				20	+1 $\frac{3}{4}$
				22	+1
				25	+1
				29	+1 $\frac{1}{2}$
				30	+1 $\frac{1}{2}$

work, records were kept of the water-level of the mainstream at C, the collecting station which could be visited most frequently. On 5 July the level was such that the beds of phanerogamic vegetation were just covered by the water and this was taken as the normal level of the mainstream. Subsequent levels were noted at Llangadock bridge and are given in Table 3. Unfortunately the river could not be inspected each day but it is believed that all significant changes are recorded.

The results of the quantitative work on the fauna are summarized in Table 4. The first collections made

on this occasion; fair numbers of *Ephemerella* and *Leuctra* turned up again and the *Hydracarina* had become rather more numerous, but there was apparently a drastic reduction in the numbers of the *Baetis* nymphs. A little random examination of the river bed showed that very few remained, and it would appear that the vast majority had been swept away by the floods of 20-27 July.

By the middle of August heavy and persistent rain had raised the river level about 3 ft. above normal, it had become very turbid and in midstream the surface current was about 5 ft. per sec. No samples

Table 4. *Quantitative fauna collections for the stony meenstream of the River Torry, summer 1950.*

Station		All figures are numbers of animals per 2500 sq.cm. sample of the river bed.													
Date (1950)	...	C	C	C	C	C	D	D	D	D	D	E	E	E	F
	...	5	10	20	24	29	1	22	7	11	5	27	13	7	Aug.
	July	July	July	July	July	Sept.	Sept.	Sept.	July	July	Aug.	July	Aug.	Aug.	Aug.
PLATYHELMIA															
Polycellis cornuta															
OLIGOCHAETA															
HERUDINEA	4				4	8		5		4	5				4
Herpobdella octoculata															2
MOLLUSCA															
Ancylastrum fluviatile															
Limnaea pereger		2		2		2		1	7	9		3			3
Hydrobia jenkinsi										6		14			3
HYDRACARINA	104	170		22	255		7	6	134	324	88	54	2	134	252
PLECOPTERA															
Leuctra spp.	72			11	43		2		27	103	45	19			42
Perla carlukiana		1													
Dinocras cephalotes		3													
Chloroperla sp.							1								
EPHMEROPTERA															
Ecdyonurus venosus	4														
Ephemerella notata	154	151	5	66	67	4	2	3	132	277	2		3	6	
Baetis spp.	87	458		12	8			6	72	90	6	63	3	9	
Caenis sp.							3					46	12	70	
HEMIPTERA															
Micronecta poweri	2							3				8	6	4	
Aphelocheirus montandoni														1	
TRICHOPTERA															
Rhyacophila sp.	2														
Glossosoma boltoni	60	62			8				39	15					
Hydropsyche sp.								1							
Plectrocnemia conspersa									1						
Lepidostoma hirtum															
Hydroptila sp.															
COLEOPTERA (imagines)															
Oreodytes septentrionalis															
Bidessus minutissimus															
Hydraena gracilis															
Elmis maugei															
Latellus volekmari										4	15				
Limnius tuberculatus									1	2					
Esolus parallelipedus															
COLEOPTERA (larvae)	76	94	17	2	27		13	2	1	18		3	1	6	
Dytiscidae												12	2	13	
Elmidae	1	18	2		7				13	48					
DIPTERA															
Hexatoma sp.	6	10	6		7		2	3	5	7	8				
Atherix sp.	1	6			1					4		2			2
Simulium spp.	9	35	31												1
Chironomidae	22	45	26	18	7		9	4	28	31	2				2
Ceratopogonidae				1	1		1					25	5	153	
Total	613	1091	365	145	445		48	40	468	949	436				
												278	49		719

could be taken under these conditions, for even where the pebble bed could be reached the force of the current made the use of the apparatus impossible. The next fauna record for station C is that of 1 September when the river fell to a level about 1 ft. above normal; this sample was taken from the flood beach region visited on 24 July and showed a very poor fauna compared with those taken in the earlier part of the summer, the total number of animals being only 48 per 2500 sq.cm. and the most numerous species was now the little beetle *Esolus parallelipipedus*. More heavy flooding occurred during September; one further sample was taken at the same point on the 22nd, the river again being about a foot above normal and the part of the stream bed investigated had therefore been covered for nearly 6 weeks. The animals now numbered only 40 per 2500 sq.cm. and a marked feature of the collection was the very small size of the specimens. The general impression is that the heavy flooding of August and September resulted in a most drastic reduction in the invertebrate population. In the case of some species their numbers are reduced by breeding out to the adult stage and many are eaten by fish and other predators; but even allowing for these factors and for great inaccuracy in the sampling, the mortality due to flooding appears to be very high. The 5 and 10 July totals (613 and 1091) have an average of 852 per 2500 sq.cm., if we assume that this figure is representative a 'pre-flood' population of 3408 macroscopic animals per sq.m. is indicated. The river is about 30 m. wide and if we assume that this population is evenly distributed, its density amounts to about 102,240 per m. of the river's length or about 100,000,000 per km. A population of 40 per 2500 sq.cm. would amount to 4,800,000 per km. These figures are, of course, largely speculative and much more data would be necessary to confirm them but there is considerable general evidence to show that heavy flooding in swift, stony rivers has a most destructive effect on the fauna. See, for instance, Butcher *et al.* (1937, p. 146) and Denham (1938).

Four quantitative samples were taken at station D and three at E, mainly for comparison with those taken at C. Generally speaking these indicate a fauna of very much the same nature as that recorded for Llangadock, and the sample taken on 5 September again revealed a very low population after the floods of the latter part of August. The single sample taken at station F on 7 August also records a fauna very similar to that seen at the stations above, but with a much greater number of *Hydrobia*. The *Gammarus zaddachi* found in abundance in the 1949 collections did not turn up in this sample, which was not taken at the same spot as that visited in 1949, but about a quarter of a mile higher up the river. No further

collecting was possible in this region on account of persistent flooding, for at the end of September the level of the water was about 6 ft. above normal.

The *Rheotanytarsus* larvae so numerous in the earlier collections did not appear in any degree of abundance in the second series. In the 8 July collection made at station E the live larvae numbered about 20 per 2500 sq.cm. and the cases about 150 per 2500 sq.cm. Later in the month and in August larvae and cases became very rare and the majority of the chironomid larvae taken in the later samples were Orthoclaadiinae.

The populations of 319–1091 per 2500 sq.cm. or 1276–4364 per sq.m. recorded for the samples taken before the summer floods compare fairly well with figures given for other rivers. Badcock (1949, p. 195) records summer month populations of 101–924 animals per 2500 sq.cm. for tributaries of the Welsh Dee. Whitehead (1935, p. 63), in his examination of the stony region of a chalk stream in Yorkshire, found that the animals numbered 15–695 per sq.cm. A considerable amount of data is given for the Tees by Butcher *et al.* (1937, pp. 128–31), the average populations for the four stations studied being 544, 847, 136 and 106 per sq.m. (p. 125). These figures are not high, and some of the individual records for the Tees are remarkably low; thus the collections made at Abbey Mill, Barnard Castle, on 30 November 1929, 27 January 1930 and 14 February 1930 indicate populations of 7, 7 and 5 animals per 2500 sq.cm. These are winter samples, but one taken in September at the same place (26 September 1930) records only 11 animals per 2500 sq.cm., a figure far below the lowest for the Towy series, and some extraordinarily low figures for summer collections are given on pp. 130 and 131 of the same paper (see, for example, the data for 26 September 1930 and 18 July 1930). The Tees is a river which is particularly liable to sudden and violent floods, and some of the samples appear to have been taken at places where the bed is largely formed of rock, a type of stream bed which supports a very poor fauna, unless there is a heavy moss growth to provide shelter.

The figures given for the Danish river Susaa by Jónasson (1948), on the other hand, are very high. Jónasson's total populations range from 8431 to 31,956 per sq.m. (tables to plates II–VII). The habitat to which the figure of 31,956 applies is very different from the type studied by the writer: at Naaby the Susaa has a luxuriant vegetation distributed over the entire width of the river and the bottom has deposits of sand and mud (Jónasson, 1948, p. 246). The fauna is of rather different type, the most numerous animals being *Gammarus pulex*, *Caenis*, trichopteran and chironomid larvae.

A considerable amount of quantitative data is available for American rivers. Murray (1938, p. 108)

gives average numbers of animals per sq.m. for thirty-three Indiana rivers and creeks, ranging from 480 to 6970; fifteen of the records are between 1000 and 2000. Some further figures of fairly similar range are given by Shockley (1949, p. 260).

Generally speaking it would appear that the bottom fauna of the main-stream of the Towy, in numbers of individuals, is reasonably rich when not depleted by floods. The impression gathered from the earlier survey of 1949 was that the fauna was rich in numbers of individuals but not so in numbers of species, for the writer's recent study of hill streams in the same neighbourhood (1948) recorded a far greater number of animal types. The fauna has many peculiarities; the numbers of water mites which occur seem remarkably high, ranging up to 324 per 2500 sq.cm. On the other hand, apart from *Glossosoma* there is a singular dearth of Trichoptera. There is also a general dearth of predatory insects, for the carnivorous Plecoptera are decidedly rare and the Dytiscidae are very poorly represented. The reasons for this are by no means clear, but there is some evidence that predatory insects tend to be rare in rivers of this type; thus only six species of Dytiscidae are recorded in the river Teifi (Jones, 1943, p. 122) and only twelve specimens of predatory Trichoptera were taken in five collections from the lower reaches of the River Dovey (Jones, 1941, p. 19). It may be that the carnivorous insects, comparatively large and active in movement, are particularly good targets for the trout and other insectivorous fish. The chief invertebrate predators of the Towy, numerically speaking, are the mites, though what they feed upon is not clear. Koenike (1909, p. 13) says that they prey upon copepods, Cladocera and ostracods, but this can hardly be the case in the habitat in question.

5. THE FOOD OF THE MINNOWS

Like other rivers of similar type the Towy supports a great number of minnows (*Phoxinus phoxinus*). The larger fish seem to prefer the clear water of the main-stream where they travel up and down in large shoals; while the smaller fish, under 20 mm. in length, seem to prefer the beds of moss and waterweed, where the surface of the water may be continually rippled by their movement. A favourite habitat of the very small fish measuring about 12 mm. is the quiet water among the stems of emergent vegetation at the river's margins. The food of the minnow has been studied by Tack (1940), Hartley (1948) and Frost (1943). Frost's paper is the chief work dealing with British minnows and is based on the examination of the gut contents of fish taken from Lake Windermere and the River Brathay. Filamentous algae, chironomid larvae and ephemeropteran nymphs were the most important foods in the fish taken from the river; diatoms, plant

debris and many other types of plant and animal food occurred in smaller amounts. Miss Frost's results are based mainly on the examination of fish of fair size, and of the 833 River Brathay fish examined, only 29 were in the 10.5–20.5 mm. group. In July 1949 it was decided to make some study of the food of the smaller minnows in the Towy to ascertain to what extent they were making use of the various types of food available. The results are summarized in Table 5. When the investigation was begun the whole gut of the fish was examined; it was soon noted, however, that in very many instances a preponderance of plant food would be discovered in the anterior part of the gut while the hind-part of the gut would contain only mineral matter and the chitinous remains of insects. It would appear that by the time the meal has reached the hind-gut vegetable matter has generally been so digested as to be unrecognizable or has been mainly absorbed while the indigestible chitinous parts of insects remain comparatively unaltered and are easily identified. Consequently an examination of the whole gut may tend to give a false impression of the amount of insect food eaten. In view of this it was decided to neglect the first records and to examine only the contents of the 'stomach' or anterior third of the gut; this is the basis of all the results in Table 5. The presence of any particular type of food was only recorded if what appeared to be a significant amount was present, thus occasional diatoms, desmids, rotifers, etc., were ignored. Hynes (1950) has recently reviewed the merits of the various methods in use for recording the nature of the gut contents of fish and concludes that for any fish with a generalized diet, provided a large number of specimens is examined, any of the commonly accepted methods will give substantially the same result.

Table 5 shows that the diet appears to vary considerably with the size of the fish and the habitat from which they are taken. The 12–14 mm. fish from station D were collected from emergent vegetation at the river bank and had been feeding mainly on Cladocera. Fish of the same size taken at station C from beds of *Ranunculus* had fed mainly on diatoms and green algae. Somewhat larger fish (16–20 mm.) collected from *Ranunculus* beds at D on 15 and 16 July had eaten a fair variety of insects, and 23 of the 50 specimens examined had a diet which was mainly animal. In contrast, fish of the same size group taken from the *Myriophyllum* beds at Dryslwyn (E, 25 July, 6 August, 7 September) appeared to show a marked preference for plant food, for the diatoms and a great variety of green algae formed the bulk of the stomach contents in most cases, only six fish having a mainly animal diet. This vegetarianism may well have been a case of necessity, for the fauna of the *Myriophyllum* beds was extremely poor, and the only animal at all common among the leaves of the milfoil was *Corixa*

Table 5. *The food of the minnows*

The figures give the actual numbers of specimens in whose stomachs the 'foods' listed in the first column occurred in significant amount.

Collection station	...	D	C	D	E	D	C
Dates	...	8 Aug. 1949	10 Aug. 1949	15 July 1949 16 July 1949	25 July 1949 6 Aug. 1949 7 Sept. 1949	13 July 1949 16 July 1949	29 Aug. 1950
Size (mm.)	...	12-14	12-14	16-20	16-20	50-65	16-20
No. examined	...	50	50	50	100	50	50
Stomach contents:							
Grit		21	40	22	74	27	22
Leaf fragments		1	.	5	1	4	.
Algae:							
Green algae of all types		26	43	23	85	39	44
<i>Sphaerocystis</i>		.	.	.	26	.	.
<i>Ulothrix</i>		.	.	.	5	1	2
<i>Stigeoclonium</i>		.	1	.	.	1	42
<i>Oedogonium</i>		4	.	4	2	29	.
<i>Bulbochaete</i>		6	13	.	6	.	.
<i>Pediastrum</i>		1	.	.	10	.	.
<i>Dictyosphaerium</i>		.	.	.	2	.	.
<i>Ankistrodesmus</i>		.	.	.	2	.	.
<i>Scenedesmus</i>		3	9	19	24	25	.
<i>Spirogyra</i>		2	1	4	8	31	.
<i>Closterium</i>		1	17	4	.	6	.
<i>Cosmarium</i>		3	8	.	28	2	.
<i>Staurastrum</i>		16	20	.	51	.	.
<i>Spondylosium</i>		.	6	.	3	.	.
<i>Hyalotheca</i>		1	8	.	1	.	.
Blue-green algae:							
<i>Phormidium</i>		3	4	1	6	1	.
<i>Oscillatoria</i>		.	.	.	4	.	.
<i>Coelosphaerium</i>		.	.	.	17	.	.
Algae not identified		.	.	.	.	1	.
Diatoms (mainly <i>Melosira</i> and <i>Fragilaria</i>)		17	42	17	78	25	.
Animals:							
Rotifera		6	3	.	.	.	.
Oligochaeta		.	4	2	2	1	4
Cladocera		40	3	3	9	.	4
Copepoda		.	1	5	4	.	4
Hydracarina		.	1	2	.	2	2
<i>Leuctra</i>		.	.	.	.	1	.
<i>Ephemerella</i>		.	.	11	.	18	.
<i>Baetis</i>		1	1	9	1	.	.
Thysanoptera		.	.	2	.	.	3
Aphididae		.	.	4	.	.	6
<i>Velia?</i>		.	.	2	.	2	.
Chironomid larvae		10	8	13	6	11	16
Chironomid pupae		.	.	2	.	2	2
<i>Simulium</i>		.	.	1	.	.	.
Remains not identified		.	1	7	.	1	4
Food mainly vegetable		11	40	15	86	34	24
Animal and vegetable food in roughly equal amount		7	6	6	4	5	20
Food mainly animal		32	4	23	6	7	4
Stomach empty		.	.	6	4	4	2

striata; these were quite numerous but the minnow does not seem to eat them.

One batch of large fish 50–56 mm. in length was examined, these were taken from the *Ranunculus* and *Callitriche* beds at station D on 13 and 16 July. They had a fairly mixed diet but the green algae seemed to form the most important food; *Spirogyra* and *Oedogonium* appeared to be relished, for in many fish the stomach was crammed with a dense mass of green filaments. As stated earlier the larger fish tend to favour the clear, flowing water; unfortunately it was not possible to catch sufficient numbers from the open water, with the apparatus available at the time, for a comparison to be made between their diet and that of the large fish netted from the water weed.

One further sample of 16–20 mm. fish was examined, on 29 August 1950, when some specimens were taken at station C. The river was in flood and the fish were collected from vegetation near the bank. The chief feature of the gut contents on this occasion was the presence of masses of the green alga *Stigeoclonium* in 42 of the 50 fish. As noted in §3, this alga became a dominant type in the wet summer of 1950; in the fish examined in 1949 it formed a significant part of the stomach contents in two instances only.

Generally speaking these results show a tendency towards a mainly vegetable diet. Of the total of 350 fish inspected 210 had stomach contents which were mainly vegetable, 48 had eaten plant and animal food in roughly equal amount and 76 had a diet which was mainly animal. How far the diet is a matter of choice and how far a matter of necessity is not clear, but it may be concluded that the abundance of minnows in rivers of this type is largely the result of an ability to exist on a mainly vegetable diet if the necessity arises. In the Towy the smaller insectivorous fish, stickleback, loach and bullhead, are far less common.

6. THE FOOD OF SOME OF THE CHARACTERISTIC INVERTEBRATE ANIMALS OF THE MAINSTREAM

In July 1949 a study was made of the feeding habits of some of the more common animals of the mainstream. The methods employed and the literature on the subject are covered in my papers on the rivers Sawdde and Rheidol (Jones, 1949*b*, 1950). The results are summarized in Table 6; all animals present in the guts were recorded, but plant foods were only noted as present when seen in what appeared to be a significant amount. The size of the animal whose diet is being studied has to be taken into account, for a dozen or so desmids may form an insignificant part of the bulky gut contents of an *Ephemera* nymph, but quite an appreciable part of the meal in a tiny *Rheotanytarsus* larva.

The *Ephemera* nymphs were feeding mainly upon

the filamentous algae *Oedogonium*, *Spirogyra* and *Microspora*, some other green algae, detritus and grit were seen in the gut contents. The *Glossosoma* larvae appeared to have rather a varied diet, including filamentous green algae and what appeared to be encrusting blue-green species. It was not possible to identify these with certainty; one appeared to be *Chamaesiphonopsis regularis* Fritsch, which has been noted as the food of *Glossosoma* in the Rheidol (Jones, 1950); the other appeared to have very thick, reddish brown sheaths and was probably *Chamaesiphon ferrugineus* Fritsch, as described by Fritsch (1929). An encrusting green alga occurred in some specimens; this could not be identified.

The adults of the beetle *Esolus* were feeding mainly on diatoms and *Scenedesmus*, the majority of the specimens also containing a fair amount of grit and nearly all being heavily parasitized with gregarines; the larvae have a very similar diet. The *Rheotanytarsus* larvae would seem to eat any of the microscopic algae on the stones around them: in a typical preparation of the gut contents would be seen a great variety of diatoms, hundreds of *Scenedesmus* and various other forms, such as *Ankistrodesmus* and other desmids. The gut would contain odd specimens of almost all the algae to be found on the stream bed, but the filamentous types did not appear to be an important part of the diet.

The *Hexatoma* larvae were the chief predatory insects met with in the period under review; the dryopid larvae and nymphs of *Ephemera* seemed to be their chief prey and two cases of cannibalism were noted. The *Gammarus zaddachi* taken at station F had been feeding very largely on the chironomid larvae; in numbers and bulk these formed by far the most important part of their diet and the 19 specimens which contained any food at all had eaten a total of approximately 82 larvae, most of them *Rheotanytarsus*.

It would appear that under the conditions of the summer of 1949 the green algae form the most important source of food for the more numerous members of the fauna. A considerable variety is available, ranging from minute forms like *Scenedesmus* to desmids of various genera and filamentous types which may develop in great quantity. The diatoms generally take second place but are more restricted in distribution and do not occur in great bulk except in very slack water, or where phanerogams or filamentous algae give shelter. How far the supply of green algae and diatoms keeps pace with demand is not easy to judge, and conditions appear to vary greatly from point to point, for the distribution of the algal growth is inclined to be very uneven. In some places the river bed may be so loaded with woolly growth that it is difficult to find the animals, while a few feet away pebbles lifted from the water may be almost clean. Generally in these 'clean' areas one

Table 6. *The food of some of the characteristic invertebrate animals of the mainstream*

The specimens were collected in July 1949; the figures give the actual numbers in which the anterior part of the gut contained significant amounts of the 'foods' listed in the first column.

	<i>Gammarus zaddachi</i>	<i>Ephemerella notata</i>	<i>Glossosoma boltoni</i>	<i>Esolus parallelo- pipedus</i> [imagines]	<i>Esolus parallelo- pipedus</i> [larvae]	<i>Rheo- tanytarsus</i> D, E, F	<i>Hexatoma</i> C
Collection station ...	F	C, D	B, C, D	C	C, D		
No. examined ...	30	30	30	30	30	30	40
Anterior part of the gut empty	11	.	2	4	.	.	3
Contents of anterior part of gut digested	.	4	2	.	.	.	12
Gut contents:							
Leaf fragments	4	3	1	.	.	.	.
Detritus and grit	5	15	15	25	6	30	.
ALGAE:							
Green algae; all types	4	26	24	13	22	26	.
<i>Ulothrix</i>	.	2	1	.	.	.	.
<i>Microspora</i>	.	7	3	.	.	1	.
<i>Stigeoclonium</i>	.	.	3	.	.	.	.
<i>Oedogonium</i>	2	15	5	.	.	3	.
<i>Bulbochaete</i>	.	.	2	.	.	.	.
<i>Ankistrodesmus</i>	.	.	2	.	.	4	.
<i>Scenedesmus</i>	2	8	2	10	19	19	.
<i>Mougeotia</i>	.	.	7	.	.	.	.
<i>Spirogyra</i>	1	18	1	1	3	1	.
<i>Staurastrum</i>	.	.	.	.	.	7	.
<i>Cosmarium</i>	1	.	.	.	.	1	.
Green algae not identified	.	.	7	7	.	.	.
<i>Chamaesiphon?</i>	.	.	3	.	.	.	.
<i>Chamaesiphonopsis?</i>	.	.	9	2	.	4	.
<i>Phormidium</i>	.	.	.	.	3	.	.
<i>Nostoc</i>	.	.	.	.	.	3	.
Diatoms	6	8	7	17	21	30	.
Animals:							
<i>Oligochaeta</i>	.	.	.	.	.	.	1
<i>Hydracarina</i>	.	.	.	.	.	.	1
<i>Leuctra</i>	1	.	.	.	.	.	.
<i>Ephemerella</i>	.	.	.	.	.	.	6
<i>Ecdyonurus</i>	.	.	.	.	.	.	1
<i>Baetis</i>	1	.	.	.	.	.	.
Dryopid larvae	.	.	.	.	.	.	7
<i>Hexatoma</i>	.	.	.	.	.	.	2
Chironomid larvae	17	.	.	.	.	.	13

finds large numbers of *Ephemerella*, chironomid larvae and other alga eaters, which suggests that these local scarcities of plant life may be due to the feeding of the insects, though other factors including the current speed and the scouring action of suspended mineral matter are also concerned.

Under the conditions of the period under review detritus would not appear to be an important source of food in the lower reaches of the river, and apart from *Leuctra fusciventris* the detritus-feeding insects are not numerous. Under autumn and winter conditions it is probable that considerable changes take place in the

general nature of the food supply, and that the green-alga feeders are replaced to a great extent by *Ecdyonurus*, *Rhithrogena*, *Heptagenia*, *Simulium*, *Anabolia* and *Halesus* and others feeding on dead leaves and amorphous decaying plant material washed into the river.

As in the Rheidol and other streams studied by the writer, the blue-green algae do not seem to play any very important part in the maintenance of the fauna. Nor do the phanerogams form an important direct source of food; eventually their leaves and stems contribute to the general supply of detritus but their

main role is to provide shelter and support for the development of a rich, local plankton of diatoms, desmids and a host of other microscopic algae. In the Rheidol the chief animal feeding on this vegetable soup is *Siphonurus lacustris*, in the Towy it is the minnow.

7. SUMMARY

1. This paper deals with an unpolluted river of moderate size, the mainstream measuring about 64 miles. The river has soft, nearly neutral water, a rather uniform and stable pebble-gravel bed and provides particularly good fishing for sewin. Trout and salmon occur also but coarse fish are rare. All observations were made during the summer months (July, August and September) of 1949 and 1950.

2. During the dry and sunny summer of 1949 the river had a rich flora including about 130 species of algae. The green algae were particularly abundant, dominant types being *Oedogonium*, *Spirogyra* and *Scenedesmus* and the desmids were well represented. In 1950 the summer was cool and wet and the flora appeared to be dominated by *Stigeoclonium*, *Ulothrix* and the diatoms.

3. The summer fauna includes about 106 species. Characteristic animals in 1949 were *Ephemerella*

notata, *Glossosoma boltoni*, *Leuctra fusciventris*, and the minnow *Phoxinus phoxinus*. *Tanytarsus* larvae of the group *Rheotanytarsus* occurred in great numbers. In July 1950 quantitative sampling of the pebble bed at four stations indicated populations of 319 to 1091 macroscopic animals per 2500 sq.cm. Severe and prolonged flooding later in the summer appeared to have a most destructive effect on the fauna; samples taken in September indicated populations of 40 to 57 animals per 2500 sq.cm.

4. A study was made of the food of minnows (*Phoxinus phoxinus*), attention being concentrated on the smaller fish (12–20 mm.) which are abundant in the river. The gut contents varied greatly with the size of the fish and the habitat from which they were taken; a marked tendency towards a vegetable diet was noticeable, of the 350 fish examined 210 having a stomach contents which was mainly vegetable and only 76 a diet in which animal food was predominant.

5. The food of some of the more numerous invertebrate animals of the mainstream was also investigated. The green algae and the diatoms appeared to be the most important types of plant food utilized. Certain species, such as *Ephemerella notata*, seem to favour the filamentous algae while others, such as the *Rheotanytarsus* larvae, prefer non-filamentous forms.

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THE 1950 CENSUS OF GANNETS (*SULA BASSANA*) ON AILSA CRAIG

By J. A. GIBSON

The gannet population of Ailsa Craig has been estimated many times, with widely varying degrees of accuracy, but the first accurate census, based on a direct count of occupied nests, was carried out in 1936 (Vevers & Fisher, 1936). Thereafter counts were made in 1937 (Vevers, Fisher, Hartley & Best, 1937), 1938 (Vevers & Fisher, 1938), 1939, 1940, 1941 and 1942 (Fisher & Vevers, 1943). There was an unavoidable interruption during the war years, but observations were continued in 1946 and counts again made in 1947 (Gibson, in the press) 1948, 1949 and 1950. From 1936 to 1942 the counts were made principally by H. G. Vevers and J. Fisher and from 1946 to 1950 principally by myself.

From 1936 to 1942 the size of the population fluctuated considerably around a mean of about 5400 pairs. In 1940 it was as high as 6232 pairs and in 1941 as low as 3518 pairs. The counts in 1947 (5383 pairs), 1948 (5190 pairs) and 1949 (4947 pairs) call for no special comment, but in 1950 there was an astounding increase, of over 1500 pairs on the 1949 population. This increase represents certain colonization from without, possibly by birds that did not breed in the previous year rather than by birds from another colony.

The census was made by means of direct counts and occupied the days 4-14 April 1950. The groupings of the colonies are much the same as those used in former years, and full details are given below.

This is the highest gannet population yet recorded for Ailsa Craig. One completely new colony (Balvaar, top ridge) was occupied and nine groups held the highest population ever counted in any year.

Fisher & Vevers (1943) arrived at an index of the amount of 'room' available for gannets on Ailsa Craig, by adding together the maximum populations that had ever been counted on each of the different

Table 1

Colony	Counts	Mean
Slidderly	142, 142	142
Slidderly, Top Ridge	202, 205	203.5
North of the Slunk	176, 174	175
Foot of the Slunk	209, 205	207
Above Ashydoo	61, 61	61
Balvaar	613, 596, 598	602.3
Balvaar, Top Ridge	120, 120	120
Balvaar to Cairn	168, 170	169
The Cairn	519, 527	523
Cairn to Mare	340, 350	345
Barrheads	431, 430	430.5
Mare	1811, 1836	1823.5
Mare, Lower Ledge	54, 54, 54	54
Mare to Stranny Point, S1	173, 174, 179	175.3
Mare to Stranny Point, S2	106, 109	107.5
Mare to Stranny Point, S3	216, 203	209.5
Mare to Stranny Point, S4	364, 354	359
Stranny Point, South Side	39, 39	39
Main Craigs, Main Part	228, 231, 225	228
Main Craigs, Top	414, 405	409.5
Main Craigs, East	108, 108	108
Main Craigs, East Top	29, 28	28.5
Main Craigs, Far East	43, 43	43
Main Craigs, Far East Top	16, 16, 16	16

Total: 6579 pairs

sections of the cliffs. By 1942 this index had reached 6836 pairs, and Fisher & Vevers stated that the cliffs could hold probably 8000 pairs. This index has now reached 8125 pairs and after my experience with the 1950 population I should say that the cliffs can hold easily 10,000 pairs without the birds having to spread on to the sloping ground at the cliff tops.

The Ailsa Craig gannet census is now carried out every year, so the 1951 count will show whether the 1950 increase in population has been maintained.

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THE DISTRIBUTION AND POPULATION DENSITY OF EARTHWORMS (LUMBRICIDAE) IN SCOTTISH PASTURE FIELDS

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1. INTRODUCTION

The investigations described here were carried out in Midlothian and in other counties of south-east Scotland. Previous work by W. Evans (1910), in what he described as the 'Forth area', showed that a number of species of earthworms occurred, and although he based many of his identifications on Friend's system of classification, which has since been proved to be inaccurate, Evans's work does indicate that 10-15 species were present in the area.

Later work (Guild, 1948) has shown that in central Scotland in 1945, under conditions of different soil type and soil fertility, a total of 14 species of earthworms, including all those found at Rothamsted (Evans & Guild, 1947, 1948) except *Allolobophora nocturna*, were present. Five species besides those found at Rothamsted were recorded. The central Scottish survey showed that the species complex and population density varied considerably between different areas. Some of the results are shown in Table 1.

Table 1. *Relation of soil type to earthworm populations (Guild, 1948)*

Soil type	Population (thousands per acre)	No. of species
Clay	163.8	9
Medium loam	226.1	9
Light loam	256.0	8
Gravelly loam	146.8	9
Alluvium	179.8	9
Natural hill pasture	51.5	5
Peaty acid soil	50.0	6
Shallow acid peaty soil	24.6	5
Light sandy	232.2	10

2. LOCATION AND NUMBER OF SAMPLING SITES

The period of survey extended from spring 1948 until autumn 1949. A total of 311 samples were taken at 31 different field sites (Table 2). The potassium permanganate wet method of sampling throughout the series was that which had been developed and proved successful for earlier work (Evans & Guild, 1947).

Table 2. *Location and number of sampling sites*

	No. of sites	No. of samples
Boghall Experimental Farm (Midlothian)	11	191
Counties in South-east Scotland	16	88
Counties in Highland area	4	32
Total	31	311

The old method of earthworm sampling was by hammering into the ground an iron sampler, 1 ft. square, and examining the resultant sample. This was soon found to be unsatisfactory, for the weight of equipment to be carried was considerable, and during the sampling, the vibration set up in the ground resulted in many of the larger worms going deep into the soil, below the level of the iron, and these were lost. As a result, the 'wet' method of sampling was evolved at Rothamsted, using the fact long known to greenkeepers, that certain chemical solutions when applied to the soil reacted on the worms and brought them to the surface. After a series of trials at Rothamsted it was found that of a large number of solutions which brought about the required reaction, potassium permanganate at the strength of $\frac{1}{4}$ oz. per gal. was the most effective, and was comparatively cheap to buy.

There are limitations to the use of this method. Only those individuals within the range of penetration of the solution are brought up. However, it has been shown that during the activity periods of the population, the individuals occur in the upper soil layers, and are therefore reached by the permanganate running down the burrows, the cracks and the crevices in the soil. When soil conditions are adverse, the worms either withdraw deep into the soil or cement themselves into aestivation cells, and are therefore unaffected by the permanganate. So this wet sampling method does not give an index of the total population, but it does give a fairly accurate estimate of the active population at the time of sampling. Seasonal variation in activity and its dependence on soil conditions of temperature and moisture have already been described (Evans & Guild, 1947).

Table 3. *Location, altitude and description of field sites*

Site	Index	County	Altitude (ft.)	Description
Boghall, Hill grazing	Bo. 1	Midlothian	1000	P.P., natural
Boghall, Leips	Bo. 2	Midlothian	900	P., 4 yr.
Boghall, Up. Fulford	Bo. 3	Midlothian	900	P.P. (twice)
Boghall, Mid. Fulford	Bo. 4	Midlothian	1000	P., 1 yr.
Boghall, Up. Lambing	Bo. 5	Midlothian	850	P.P.
Boghall, House Park	Bo. 6	Midlothian	650	P., 2 yr.; P., 4 yr.
Boghall, Cow Loan	Bo. 7	Midlothian	600	P., 1 yr.
Boghall, Anchordales	Bo. 8	Midlothian	650	P., 1 yr.; P., 3 yr.
Boghall, March Park	Bo. 9	Midlothian	600	P., 2 yr.
Boghall, Hay Knowes	Bo. 10	Midlothian	550	P., 2 yr.
Boghall, Threshy Park	Bo. 11	Midlothian	600	P., 3 yr.
Braehead	M. 1	Midlothian	300	P., 2 yr.
Haugh Head	M. 2.	Midlothian	550	P., 4 yr.
Penicuik 1	M. 3	Midlothian	800	P.P.
Penicuik 2	M. 4	Midlothian	800	P.P. (very acid)
Penicuik 3	M. 5	Midlothian	800	P.P.
Ulston	R. 1.	Roxburgh	550	P.P.
Grahams Law	R. 2	Roxburgh	200	P., 1 yr.
Wedderlie	B. 1	Berwick	660	P.P.
Cattle Shiel	B. 2	Berwick	650	P.P.
Gavinton	B. 3	Berwick	400	P.P.
Halyburton	B. 4	Berwick	600	P.P.
Nisbet Hill	B. 5	Berwick	250	P.P.
Traquair	P. 1	Peebles	600	P.P.
Quair	P. 2	Peebles	550	P., 3 yr.
Lauriston A	W.L. 1	West Lothian	200	P.P.
Lauriston B	W.L. 2	West Lothian	200	P.P.
Glentarf	Pt. 1	Perthshire	550	P.P.
Lephinmore	A. 1	Argyll	S.L.	P.P.
Dundonnell A	Ro. 1	Ross-shire	S.L.	P., 1 yr.
Dundonnell B	Ro. 2	Ross-shire	S.L.	P.P.

P.P.=permanent pasture; P.=rotation pasture field or pasture field of less than seven years establishment; the figures '1 yr. 2 yr. 3 yr.' etc. refer to the year of growth of the pasture at the time of sampling.

'Twice' means that the field was sampled in both the 1948 and 1949 surveys.

S.L.=sea-level.

Although the sites* in the present series were not all sampled at the same time, sampling was carried out only at the times of year and under climatic conditions which had been shown by previous work to be suitable for obtaining a high proportion of the active population.

The field sites and samples are divided into the following categories:

(a) *Boghall Experimental Farm*. Eleven fields were sampled, three being permanent pasture (two treated and one natural), and eight rotation grass of from 1 to 5 years establishment. The sampling was

* A field 'site' is taken to mean an enclosed field or an unenclosed pasture area, not less than 4 acres in extent, on which a series of samples was taken to assess the population of the area. The minimum number of samples per 'site' was four. For the majority of sites there was more than the minimum number. The amount of variation between samples taken within the same site is being studied in a further more detailed survey.

divided into two surveys, the first at the end of March 1948 (five fields, 64 samples) and the second in September 1949 (nine fields, 127 samples).

(b) *Counties in south-east Scotland*. Sixteen field sites located in Midlothian (5), Roxburgh (2), Berwick (5), Peebles (2) and West Lothian (2). The majority were permanent pastures and were sampled in the April of 1948.

(c) *Counties in the Highland area*.† Four field sites located north of the popularly termed 'Highland Line'—no accurate geographical definition can be given—one each in Perthshire and Argyll and two in Ross-shire. These sites were sampled in September 1949.

† The Highland area is generally taken to comprise the crofting counties of Shetland, Orkney, Caithness, Sutherland, Ross and Cromarty, Inverness, Argyll and the highland area of Perthshire. (Dept. Agric. Scotland, 1947).

3. SPECIES RECORDED

In the course of this work fifteen species of Lumbricidae belonging to seven genera were recorded (Table 4). Two of the species, *Dendrobaena mammalis* and *Eiseniella tetraedra*, had not been recorded in the 1945 survey, but one of the species found in 1945, *Allolobophora icterica*, was not recorded in the present series. The last species is believed to be one recently introduced to this country (Cernosvitov & Evans, 1947), and to be of very local distribution.

Allolobophora nocturna (Evans) was not recorded in this series, in a total of over 5000 specimens. The species was also absent from the 1945 survey and so far has not been recorded from Scotland. The same is true of the species *Eisenia foetida* (Savigny) which, with the exception of a single specimen, has never been found in natural field populations. *Allolobophora nocturna*, on the other hand, has been found to be a very common field species in England.

Table 4. *Species recorded in Scotland, 1948-49*

<i>*Allolobophora longa</i>	<i>Dendrobaena mammalis</i> (Savigny)	<i>Lumbricus castaneus</i> (Savigny)
<i>A. caliginosa</i> (Savigny)	<i>D. octaedra</i> (Savigny)	<i>L. festivus</i> (Savigny)
<i>A. chlorotica</i> (Savigny)	<i>D. rubida</i> (Savigny)	<i>L. rubellus</i> (Hoffmeister)
<i>Eisenia rosea</i> (Savigny)	<i>Octolasion cyaneum</i> (Savigny)	<i>L. terrestris</i> (L.)
<i>Eiseniella tetraedra</i> (Savigny)	<i>O. lacteum</i> (Oerley)	<i>Bimastus eiseni</i> (Levinsen)

**A. longa* = *A. terrestris* (Savigny) var. *longa* (Ude) (Cernosvitov & Evans, 1947).

3. SPECIES COMPLEX

Of the fifteen species recorded in this survey the greatest number in any single field population was found to be ten, and the lowest to be four (Table 5). It appears that this number is not necessarily related to the type or age of the pasture or field. Both permanent and rotation pastures were found to have populations with from five to ten different species.

Of the 31 fields sampled, three had a species complex of ten species, six of nine species, five of eight species, four of seven species, seven of six species, five of five species and one site with only four species. There was no apparent grouping of species according to counties or areas: Boghall farm had field populations with from five to ten species; south-eastern counties had field populations with from five to ten species; the Highland area had field populations with from four to nine species.

The range of five to ten species appears to be fairly constant in this country. In central Scotland (1945) the population range was also found to be five to ten species and at Rothamsted the range was five to eight species (Evans & Guild, 1947). As sampling areas increase in size, or as fields are grouped together, so the number of species present may increase.

The four species most widely distributed are *Allolobophora caliginosa* and *Lumbricus terrestris*, which

were both present on all of the 31 sites; *L. rubellus* which was present on 30 sites and *Allolobophora longa* present on 27 sites. The succeeding sections will show that these species are not necessarily present in equal numbers in field populations.

These four species appear to be tolerant of a wide range of pasture types, altitude and soil acidity. All four were found in appreciable numbers and formed high percentages of populations on pasture fields of varying type even at altitudes of over 1000 ft. (Tables 6-8). This is not the highest elevation recorded for any one of them, for W. Evans found an individual *A. caliginosa* at an elevation of 1500 ft. on the Braes of Balquidder in Perthshire.

It is probable that in Britain, where the maximum altitude is 3000-4000 ft., the limiting factor is not altitude itself—although the low temperatures at higher altitudes will undoubtedly reduce earthworm metabolism and breeding—but the lack of suitable soil habitats at elevations much above 1500-2000 ft.

By recording one *A. chlorotica* on Stuc-a-Chroin at 3189 ft., an unspecified lumbricid on Ben Lomond at 3192 ft. and a single *Dendrobaena mammalis* on the summit of Ben Lawers at 4000 ft. W. Evans showed that altitude itself is not a complete limiting factor.

My field sites varied from first-class grazings down to rough acid pastures and natural hill pastures, and there was also a wide range of soil acidity between different sites, but nevertheless the acidity did not appear to be correlated with the presence or absence of the above-mentioned species. It should be noted that in the 1945 survey both *Allolobophora caliginosa* and *A. longa* were absent from the three very acid peaty areas, where the pH was in the region of 4.0-4.5, and that *Lumbricus terrestris* and *L. rubellus* were both present.

Thus these four common field species in Scotland are found to exist in all field populations under the range of conditions normally encountered in agriculture; though under conditions of high acidity frequently found in typical hill farming areas, i.e. peat moss, peat bog, etc., *A. caliginosa* and *A. longa* are likely to be absent.

Three other common field species, *A. chlorotica*, *Eisenia rosea* and *Lumbricus castaneus* were also found to be widely distributed throughout the range of soil conditions sampled, though to a lesser extent than the three previously mentioned species. *Allolobophora*

Table 5. *Field sites and species present*

Site	<i>Allolobophora longa</i>	<i>A. caliginosa</i>	<i>A. chlorotica</i>	<i>Eisenia rosea</i>	<i>Lumbricus castaneus</i>	<i>L. festivus</i>	<i>L. rubellus</i>	<i>L. terrestris</i>	<i>Octolasion lacteum</i>	<i>O. cyaneum</i>	<i>Dendrobaena rubida</i>	<i>D. mammalis</i>	<i>D. octaedra</i>	<i>Bimastus eiseni</i>	<i>Eiseniella tetraedra</i>	Total species
Bo. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9
Bo. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	10
Bo. 3	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	10
Bo. 4	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9
Bo. 5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	5
Bo. 6	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9
Bo. 7	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	8
Bo. 8	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	7
Bo. 9	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	5
Bo. 10	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	7
Bo. 11	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	8
M. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
M. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
M. 3	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	8
M. 5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	4
M. 4	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	5
R. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9
R. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
B. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	5
B. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
B. 3	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
B. 4	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	5
B. 5	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	7
P. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	10
P. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9
WL. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	7
WL. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
A. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	4
Pt. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
Ro. 1	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	6
Ro. 2	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	9

chlorotica occurred on a total of 22 sites, in all counties of the present series except Argyll; *Eisenia rosea* on 20 sites in all counties except West Lothian and Argyll; and *Lumbricus castaneus* on 15 sites, in all counties except Perthshire. Although these species were not recorded in these particular counties in the present series, it is very likely that future work will show them to be present.

The species *Allolobophora chlorotica* and *Eisenia rosea*, like *Allolobophora caliginosa* and *A. longa*, were absent or in very low numbers under peaty soil conditions where acidity was high (a fact which had been noted also in the 1945 survey), e.g. on the acid pastures of B.1, M.4, B.2 and A.1. *Lumbricus castaneus*, however, like the other members of its genus, *L. terrestris* and *L. rubellus*, is tolerant of a higher degree of acidity and was present on three of these acid sites, Bo. 1, B.2 and A.1.

Octolasion cyaneum might also be included in this group, as it occurred on 16 sites, but unlike the species above mentioned it was not recorded on any of the four sites in the Highland area. The other species of this genus, *O. lacteum*, was recorded only twice; in the Highland area at Pt. 1, and one at Boghall. In the 1945 survey this species was found both in the Carse of Stirling and at Ballochraggan, and so it would appear that the two *Octolasion* species are fairly widely distributed in central and southern Scotland, but never in large numbers. Similar results were obtained at Rothamsted (Evans & Guild, 1947).

The remaining recorded species of the genus *Lumbricus*, *L. festivus*, was found on eight field sites. It was recorded only once in the 1945 survey, as a component of an alluvial soil population near Stirling, but in the present series it was found on four permanent pastures at Boghall (Bo. 1, 2, 3 and 5) with altitudes varying from 800 to 1000 ft., on permanent pastures at M.4 (800 ft.) and R.1 (550 ft.) and on a third-year pasture at P.2 (550 ft.). *L. festivus* was not recorded from Rothamsted, and the scattered records obtained in England indicated that the species is scarce and localized. The present Scottish records now indicate that the species is more widely distributed than was formerly supposed.

Three species of the genus *Dendrobaena* were recorded. *D. rubida* which occurred on a total of nine sites, in five counties, and *D. octaedra* on single sites in Midlothian and Ross-shire, were both recorded in 1945. *D. mammalis* was newly recorded in the present series, on eight sites, in Midlothian, Berwick and Roxburgh.

D. rubida was mainly confined to the rougher and more acid pastures, irrespective of altitude, and appears to be widely distributed—on three sites at Boghall, and at M.4, P.1, W.L.1, Pt.1, and Ro.1 and 2. *D. octaedra*, which was widespread in the 1945 survey, was recorded only twice in the present series: on the natural hill pasture Bo. 1, and under similar pasture conditions in Ross-shire at Ro.2. *D. mammalis*, absent from the 1945 survey, was recorded from

widely differing sites in the present series: five permanent pastures, at Boghall and elsewhere, and three rotation pastures in Midlothian. Judging from these results this species does not appear to be confined to permanent pastures as do the other two species of this genus.

The single recorded species of the genus *Bimastus*, *B. eiseni*, was recorded in 1945 under very acid soil conditions at Pendreich Reservoir, Stirling, in fairly high numbers; but in the present series only a single specimen was obtained, and that was from a good rotation pasture, B.10. So the results available for this species are insufficient to come to any conclusions concerning its ecology.

The remaining species recorded in this series, *Eisenella tetraedra*, was described by Beddard (1895) and by Cernovitov & Evans (1947) as being amphibious, or occurring in damp and wet soil, in the immediate vicinity of streams, ponds, etc., In the present series, however, the species was recorded in numbers from a permanent pasture site in Perthshire, Pt. 1. This site was on a gently sloping hillside at an altitude of 550 ft. and the soil was moist, but certainly not wet, and some distance from the nearest source of water.

4. FIELD POPULATIONS: NUMBERS AND SPECIES PROPORTIONS

For convenience in discussion the total samplings can be divided into three parts: (a) Boghall Experimental Farm; (b) counties in south-east Scotland; (c) sites in the Highland area.

(a) *Boghall Farm*. This typical semi-upland farm lies on the eastern side of the Pentland Hills, and the fields sampled are all between 500 and 1000 ft. approximately. The soil varies from heavy loam, and in parts clay, at the lower levels, to light loam on the upper fields. There is also variation in the soil type between and within individual fields. The rainfall at the steading (640 ft.) averages 32.5 in. per annum.

*Total population densities.** The 1945 survey showed that there were considerable differences between the populations of different soil types in the Stirling area, from 147,000 per acre on gravelly sand, to 163,800 on clay up to 226,000 on medium loam and 356,000 on light loam.

Results at Boghall showed a similar range in population between fields differing in treatment, attitude and soil type. The many variable factors made it difficult to relate difference in populations or in species complex to any single factor such as soil type or age of pasture but in some cases general conclusions could be drawn.

Table 6 summarizes the total populations on the

* A 'total population' density is the total of both adult and immature stages of all species within that population.

Boghall field, with separate figures for the more important component species. The lowest population density was 60,000 per acre, and as this was recorded from an area of natural hill grass, it was much as expected, when compared with population figures obtained on similar rough-grass habitats (Guild, 1948). The highest density was 341,000 per acre on the fertile 4-year pasture Bo. 6.

From the 1948 survey there is some indication that there may be some relationships between population density and age of pasture.

On the 1- and 2-year pastures, (138,000 and 134,000 per acre respectively) where the faunas were recovering from the effects of mechanical cultivations, the populations were lower than that of the 3-year field (160,000 per acre), which in turn was lower than that of the permanent pasture Bo.3 (180,000 per acre). While these differences are probably real, the variable factors in the ecology of the different sites makes a strict interpretation of significance figures, on an age-of-pasture basis, of doubtful value.

The second survey in 1949 showed that the 1- and 2-year fields again had low populations (114,000 on Bo.4, 120,000 on Bo.7, 135,000 on Bo.9 and 120,000 on Bo.11), but the 3-year pasture Bo.8 had a lower population than 18 months previously (105,600 compared with 138,000). An increase would have been expected here, following the further period for establishment and building up of the population.

The drop from 180,000 to 125,000 on the permanent pasture field Bo.3 was also unexpected, there having been no observable change in the habitat to account for it, but the differences between the two 4-year pastures, 113,400 on Bo.2 and 341,000 on Bo.6, may be partially explained by the higher altitude (1000 ft.) and thinner and less fertile soil of the former.

Assuming that the spring sampling figures are normally rather lower than the corresponding autumn figures (Evans & Guild, 1947), it is nevertheless difficult to explain the drop in the populations of the fields Bo.3 and 8 over the 18-month period. An increase in population would certainly have been expected in the latter case. The big increase in the rotation grass population of Bo.6 from 134,000 to 341,000 over the same period is quite remarkable, but this was due almost entirely to one species, as will be shown later.

From the available figures (the present series and the 1945 surveys) it can be said that during the periods of maximum activity in autumn and spring field populations in Scotland, under normal agricultural conditions, exceed 100,000–120,000 per acre and may reach much higher figures, up to and over 300,000 per acre. Variation between populations is considerable, due to wide variation in field conditions, which affect the total and the individual species numbers.

An analysis of the numbers and the proportions of the different species explains many of the differences

Table 6. *Boghall*—total population densities (in thousands per acre)

Field	Total density	<i>Allolobophora longa</i>	<i>Allolobophora caliginosa</i>	Total	Percentage	<i>Lumbricus</i> spp.	
		no.	no.			no.	Percentage
Spring 1948							
Bo. 1	60.0	10.6	37.2	47.8	79.6	8.0	14.0
Bo. 3	180.0	36.0	108.5	144.5	80.3	27.5	15.3
Bo. 6	134.0	34.8	57.6	92.4	69.0	32.5	24.3
Bo. 8	138.0	50.8	42.8	93.6	67.8	12.4	9.0
Bo. 11	160.0	64.3	67.7	132.0	82.5	23.2	14.6
Autumn 1949							
Bo. 2	113.4	58.9	33.0	91.9	81.0	18.6	16.4
Bo. 3	125.0	32.2	41.1	73.4	58.8	48.5	39.3
Bo. 4	114.0	12.1	73.9	86.0	75.4	25.1	21.6
Bo. 5	177.0	118.1	10.8	128.9	72.8	47.4	26.8
Bo. 6	341.0	252.7	16.4	269.1	78.9	72.0	21.0
Bo. 7	120.0	67.6	35.6	103.2	86.0	21.6	12.7
Bo. 8	105.6	62.7	11.4	74.1	70.2	20.4	19.3
Bo. 9	135.0	79.8	37.8	117.6	87.1	16.2	12.0
Bo. 10	120.0	38.5	38.0	76.5	63.8	17.5	14.6

Lumbricus spp. = the total of the four species found at Boghall.

between populations which are not obvious by looking at the total numbers themselves.

Two of the common species, *Allolobophora longa* and *A. caliginosa*, were the most important components, either singly or together, of all the populations sampled (Table 6). In several cases their numbers were appreciable, e.g. *A. longa* totalled 252,700 per acre on Bo. 6 and *A. caliginosa* totalled 108,500 per acre on Bo. 3 (1948), and the highest combined total was 269,100 per acre on Bo. 6 (1949). Together the two species totalled over 60% of each of the fourteen populations (58.8% in one case), exceeding 75% in three of them and 80% in two others. The combined total exceeded 70,000 per acre in all populations except that of the natural hill area (47.8) and in five cases exceeded 100,000 per acre.

Although the combined percentage was maintained at or above 60%, the two species were not necessarily of equal importance. Both species had numbers as low as 10,000 per acre and as high as 100,000 per acre (and with *A. longa* on Bo. 6 1949 very much higher), and both species formed high and low percentages in different populations, *A. longa* being as low as 10.6% and as high as 74.1% and *A. caliginosa* with a similar range, 4.8–64.8%.

Normal field populations appear to have one or other of these two species as the dominant species, and over the farm as a whole *A. longa* was dominant in eight of the populations (exceeding 50% in six cases), while *A. caliginosa* was dominant in the remaining six (exceeding 50% in three cases), though of course the margin of dominance varied considerably. Dominance does not appear to be determined by the age of the pasture, for on five of the eight young grass fields

of from 1 to 3-years' establishment *A. longa* was dominant, and *A. caliginosa* on the remaining three.

It was noted earlier that the total population had diminished unexpectedly over the 18-month period between the samplings on the two fields Bo. 3 and 8. These reductions were primarily due to reductions in the numbers of *A. caliginosa*.

The natural hill grazing Bo. 1 with a population of only 60,000 per acre showed how population numbers are affected by low fertility and herbage deterioration. In this case the soil was not markedly acid, and the population, though low in number, nevertheless comprised mainly the common pasture species. *A. caliginosa* and *A. longa* were still the most numerous species. Two species commonly found in acid soil populations, *Dendrobaena* and *D. octaedra*, had established themselves in this area, but only in low numbers—less than a thousand per acre.

Four species of the genus *Lumbricus* were present on Boghall: *L. terrestris*, *L. rubellus*, *L. castaneus* and *L. festivus*. Determination of the species to which immature *Lumbricus* specimens belonged was by segment counts (Evans, 1946), as far as possible. Fairly accurate determinations could be made in all cases except where *L. rubellus* and *L. festivus* occurred in the same population. In such cases the only solution was to apportion the suspected immatures of these two species according to the number of adults. *L. terrestris* and *L. rubellus* were present on all fields; *L. castaneus* was not so widely distributed, being present only on five fields, and *L. festivus* on four. Individually the species did not form a high proportion of any population, not even on the natural hill area, and only in a few cases did any single species exceed

20% of a population (*L. terrestris* once on Bo. 6, 1948, and *L. rubellus* once on Bo. 3, 1949). In most cases individual *Lumbricus* species, when present, formed less than 10% of the population.

If the genus is considered as a whole, it is seen that the total *Lumbricus* formed an appreciable, though not a major part, of all populations, both by numbers and by percentage. The percentage varied from 9.0 to 39.3%, but omitting these two extreme values, a more normal range would be 10–25%. The range in numbers was much greater, and excluding the figure of 8000 per acre on the natural hill area, was from 12,000 to 72,000 per acre.

The six populations with the highest *Lumbricus* numbers per acre—exceeding 20% of the population in five cases—occurred on the upper light soil fields, and in each case the numbers exceeded 25,000 per acre, while on the lower fields, Bo. 7–11, on no field did the genus represent more than 20% of the population or the numbers exceed 25,000 per acre. The ‘common earthworm’, *L. terrestris*, was the most numerous within the genus, and although it did not approach either *A. longa* or *A. caliginosa* in importance the species formed 10% or over of the total population in all three cases, and was the dominant *Lumbricus* in ten population, *L. rubellus* superseding it in the other three. *L. castaneus* and *L. festivus*, although present in several populations, only represented a few thousands per acre.

These results show that *Lumbricus* species are more numerous and form a higher proportion of the population on the lighter soils (as was also noted in the 1945 survey).

The six species so far described together comprised over 93% of the total population in all but three cases. In each of these three cases *Allolobophora chlorotica* assumed some importance, 9.1, 18.4 and 10.6% respectively; but apart from these *A. chlorotica* was not an important species.

The remaining Boghall species were variously distributed, but individually or collectively they never formed more than 5% of any population, and at the most represented only a few thousands per acre, figures which are very low compared with those for *A. longa*, etc.

(b) Counties in south-east Scotland

This area is taken to mean the counties of Midlothian, West Lothian, Peebles, Roxburgh and Berwick, and the 16 field sites occurred over a wider range than at Boghall.

In the majority of the south-east populations numbers were within the same range as those at Boghall, 100,000–200,000 per acre. Only one site exceeded 300,000 per acre (M. 5), and only three others exceeded 200,000 per acre. A single population was below 100,000 per acre.

Variation within and between populations was greater than at Boghall, but this was to be expected due to the greater ecological variation.

A. longa and *A. caliginosa* again formed substantial proportions of all populations, together totalling 50% or over in 11 of the 16 cases (two at 49%), and over 60% in six of these. The combined numbers exceeded 100,000 per acre on five sites. Two relatively low figures were obtained—29% on M. 4 and 17% on B. 4, but in the former case the site was a very acid rough pasture, and in the latter a rough permanent hill pasture. *A. longa* was not of the same general importance in the south-east area as it was on the more localized areas of Boghall, for it was dominant in only four of the populations, and in fact formed less than 10% in five populations and was absent altogether from two others. *A. caliginosa*, however, was more consistent, being dominant in nine populations, and forming 20–50% in all populations sampled except two.

The distribution of the *Lumbricus* species was extremely variable, from 11.7 to 78.6%; but on 11 of the 16 sites the proportion was one-third or over of the population, with numbers up to 124,800 per acre, showing that over a wide area the genus attains some degree of numerical importance. In general the *Lumbricus* numbers were higher than those at Boghall, and the highest numbers per acre were obtained on the medium or light soil sites of M. 3–5 and B. 1–5.

In all populations in the south-east, *A. caliginosa*, *A. longa* and the *Lumbricus* species together formed over 80%, and in ten cases over 90%. The remaining species formed from 2.8 up to 19.7%, but as at Boghall, were variable in distribution and not of great numerical importance. Of these minor species *A. chlorotica* was the most numerous, particularly where the percentage exceeded 12%, being 9.5% on M. 5, 10% on P. 1 and 18.2% on W. L. 1.

The three sites M. 3, 4 and 5 were of interest as they had the highest populations of any in the south-east area, 235,800, 220,800 and 301,200 per acre. These three pastures were immediately adjacent to one another and occurred at an altitude of 800 ft. on medium loam soil. M. 3 and 5 were fertile pasture fields, but M. 4 was very acid, with scattered reeds and rushes, and under such conditions a low population on this site would not have been unexpected. However, although *A. longa* was not numerous (6000 per acre), *A. caliginosa* was well represented (58,500 per acre), and the *Lumbricus* species tolerated the acidity and totalled 124,800 per acre—the highest figure recorded in this series or at Boghall. This high population was due mainly to *L. rubellus*, which was dominant species with 96,000 per acre. It has been noted before (Guild, 1948) that this species is more acid-tolerant than the majority of common field

Table 7. *South-east Scotland—total populations in thousands per acre*

Field	Total density	<i>Allolobophora longa</i>	<i>Allolobophora caliginosa</i>	Total	Percentage	<i>Lumbricus</i> spp.	
		no.	no.			no.	Percentage
M. 1	132.0	42.8	42.8	85.6	64.8	42.8	32.4
M. 2	88.8	30.1	15.0	45.1	50.8	40.6	45.7
M. 3	235.8	73.3	87.0	160.3	68.0	53.3	22.6
M. 4	220.8	6.0	58.5	64.5	29.2	124.8	56.5
M. 5	301.2	79.6	69.0	148.7	49.3	112.3	37.3
R. 1	192.6	89.3	68.2	157.5	81.7	22.5	11.7
R. 2	114.0	17.3	72.3	89.6	78.8	15.9	13.9
B. 1	130.8	.	54.2	54.2	41.4	55.1	42.1
B. 2	114.0	18.0	46.5	64.5	55.8	39.0	34.2
B. 3	162.0	.	67.6	67.6	41.7	79.5	49.1
B. 4	114.0	1.5	18.2	19.7	17.3	89.6	78.6
B. 5	205.8	19.6	86.0	105.6	51.3	90.1	43.8
P. 1	129.6	17.5	61.6	79.1	61.0	25.0	19.3
P. 2	169.8	88.6	49.6	138.2	81.4	22.6	13.3
W.L. 1	139.6	4.5	64.2	68.7	49.2	55.6	39.8
W.L. 2	115.2	1.5	46.4	47.9	41.6	44.9	39.0

Lumbricus spp. = the total of the four species.

species and frequently becomes the dominant species in acid soils. The acid nature of this site was further shown by the relative abundance of *Dendrobaena rubida*—36,000 per acre—a figure which is high for this species. *D. rubida* had been shown to be abundant on certain acid soils in the 1945 survey.

The effects of mechanical cultivations were well shown in the two populations R. 1 and 2, the former being a good permanent pasture and the latter a 1st-year grass field. The major difference between the populations was that on R. 1 *A. longa* was numerous and totalled 89,200 per acre, whereas on the equally fertile young grass field R. 2 it numbered only 17,200 per acre. It has been previously noted that this species, one of the larger ones, occurred in low numbers on young pastures, due possibly to mechanical damage (Evans & Guild, 1947), as a result of which several years would be required before high numbers could again be built up. This has not always been found to be the case, but such an effect is probably seen in the differences between these two populations.

The small Berwickshire series B. 1–5 showed how altitude and exposure can reduce population numbers on sites with similar soil conditions. The fields were all permanent hill pastures, containing a proportion of *Festuca ovina*, but only a thin basal mat of herbage nevertheless, and the soil was light loam throughout. The three higher and more exposed areas B. 1, 2 and 4 had populations of 130,800, 114,000 and 114,000 per acre respectively. *Allolobophora longa* was not an important species at all in this particular area, and very little casting was ever seen on these sites. On B. 1 and 3 the species were absent altogether, these being the only records of its complete absence from a field population in the present series.

A similar reduction in numbers was noted in West Lothian, where the two adjacent areas W.L. 1 and W.L. 2 had populations of 115,000 and 140,000 per acre respectively. The only observable difference between these two areas was the higher acidity and rougher herbage of W.L. 1. Again *A. longa* was of reduced importance in this area. In each of the populations where *A. longa* was either absent or present in low numbers, *A. caliginosa* on the other hand was relatively abundant, and maintained the high combined proportion of the population, as noted earlier.

(c) Sites in the Highland area

Brief reference will be made to sites Pt. 1, A. 1, and Ro. 1 and 2, and a fuller discussion of the results will be deferred until more results are to hand.

The figures in general were low, and on A. 1—a poor-quality permanent pasture with thin, stony and probably acid soil—on the shores of Loch Fyne, the low fertility was reflected by the very low population, 30,000 per acre. This figure is the lowest recorded on agricultural land in Scotland. There were only four species present, of which *A. caliginosa* formed 35 % or 10,500 per acre while of the three *Lumbricus* species present, *L. rubellus* was dominant (42.5 %). Although the population was so low, there were no *Dendrobaena* species present as on other areas of low fertility.

By contrast, the permanent pasture Pt. 1 appeared to have quite a high population—106,800 per acre. This site, at about 500 ft., was a more fertile and productive pasture than A. 1, but nevertheless the population was low compared with those of Boghall and elsewhere. *Allolobophora longa* was again absent

Table 8. *Highland area—populations densities in thousands per acre and proportions*

Total density in thousands per acre		Pt. 1	A. 1.	Ro. 1	Ro. 2
<i>Allolobophora longa</i> : Nos.	.	.	.	24.7	1.0
	Percentage	.	.	16.3	1.4
<i>A. caliginosa</i> : Nos.	19.5	10.5	40.5	21.2	
	Percentage	18.3	35.0	26.7	29.5
<i>Lumbricus</i> spp.: Nos.	64.7	19.5	70.0	39.0	
	Percentage	60.6	65.0	46.1	54.2
Others:		21.1	.	13.9	16.3
	Percentage				

and *A. caliginosa* numbered only 19,500 per acre, but the *Lumbricus* totalled 64,700 per acre, of which *L. rubellus*, as on A. 1, formed the greater part, nearly 60,000 per acre.

The species complex was richer than on A. 1 (Table 5) and included the interesting species *Eiseniella tetraedra*, representing 7% of the population or 7,500 per acre. Further samplings in the area will determine whether the species is localized or widespread.

The two Ross-shire sites were a re-seeded 2-year ryegrass pasture, Ro. 1, on fairly deep, fertile soil, with a total population density of 151,800 per acre; and the adjacent area Ro. 2, which was of rough unimproved pasture (mainly *Festuca ovina*) and very acid, with a population only half that of Ro. 1—72,000 per acre. The former figure is similar to those of many other areas.

Allolobophora longa was of reduced importance in this area, only 24,700 per acre (16.3%) on Ro. 1 and only about 1% of the population on Ro. 2. *A. caliginosa* was more numerous, with 40,500 per acre (26.7%) on Ro. 1 and 21,100 per acre—about one-third the population—on Ro. 2.

The *Lumbricus* species formed the most important group—70,000 per acre (46.1%) on Ro. 1, which is a high figure, and 39,000 per acre (52.2%) on Ro. 2. In both cases *L. rubellus* was dominant.

The indications are that on Highland pastures where the soil is generally acid and of low fertility, and the herbage is rough (the result of generations of selective sheep grazing without pasture treatment), as typified by A. 1 and Ro. 2, the populations are much lower than in other parts of the country. *Allolobophora longa* ceases to be an important species in the population and even the cosmopolitan *A. caliginosa* is of

reduced importance. The populations are mainly composed of the *Lumbricus* genus, with *L. rubellus* the dominant species.

5. SUMMARY

1. Observations on earthworm (Lumbricidae) populations have been made in South-east Scotland to determine the distribution, species complex, population density and the variation between populations in the field, in different areas and under different ecological conditions. The survey shows that fifteen species are present, representing seven genera and including all those species recorded in the 1945 survey in central Scotland, except *Allolobophora icterica*, and including a further two not recorded in 1945—*Dendrobaena mammalis* and *Eiseniella tetraedra*.

2. The maximum number of species occurring in any single field population is shown to be ten, seven or eight being the more usual number, and of these *Allolobophora longa*, *A. caliginosa*, *Lumbricus terrestris* and *L. rubellus* are common to the majority of populations.

3. During the periods of maximum activity field populations exceed 100,000 per acre and often reach much higher numbers, up to 200,000 or even 300,000 per acre.

4. *Allolobophora longa* and *A. caliginosa* are the dominant species in nearly all cases and together form over 50% of the population by numbers. When the numbers for the species of *Lumbricus* are added, the combined total exceeds 80% of all populations and very often exceeds 90%. Of the remaining species, which are present in lesser proportions, only *Allolobophora chlorotica* exceeds 10% by numbers, and that only in a few of the populations.

5. There does not appear to be any definite relationship between the age of a pasture and the number and type of species present in the population; for although the population numbers are frequently higher on permanent pastures than on rotation pastures, the larger species such as *A. longa* and *Lumbricus terrestris* are not always present in reduced numbers compared with smaller sized species. Acid soils, however, appears to reduce the relative abundance of *Allolobophora longa* and *A. caliginosa*, and consequently the *Lumbricus* species form a greater proportion of the population under what would be considered to be less favourable soil conditions, such as acidity, exposure and thinness of soil at higher altitudes.

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THE EFFECT OF VEGETATION ON THE BREEDING OF NEWTS, *MOLGE CRISTATA* AND *MOLGE VULGARIS*

By R. S. WIMPENNY

According to Stolte (1921*a*, *b*), in some aquatic oligochaetes (Naiads) sexual reproduction is governed by the oxygen given off by algae. Here there is an optimum, deficiency or superfluity of oxygen being unfavourable. Miyazaki (1938), dealing with oysters, has reported a substance contained in green algae which produces spawning in the male oyster.

In the observed breeding habits of fishes, there is frequent reference to association with aquatic vegetation. Among the fresh-water fishes for instance, sticklebacks, the bowfin (Boulenger, 1931) and the gourami (cited by Meek, 1916) are known to make nests among water plants, while the common carp, *Cyprinus carpio* (Boulenger, 1931) and the European catfish, *Silurus glanis* (Meek, 1916), both deposit eggs on water plants. Among marine fishes wrasses and the Saragossa fish (Boulenger, 1931) nest among seaweed and the eggs of skates and rays are anchored among weeds.

To these instances of the association of a special type of environment with the reproduction of aquatic animals I must add a casual observation of my own on a fresh-water vertebrate. I noticed, one spring, that common newts kept for some days in a gold-fish bowl with clean water and no weed made no attempt to spawn, but proceeded to deposit ova almost immediately after the introduction of the pond-weed *Elodea canadensis*. During the course of experiments shortly to be described and which are prompted by this casual observation, Dr Harding of the British Museum informed me that he had had a similar experience with *Amblystoma*. I quote from his letter with his permission. 'The female had been in the water for some months... There was no weed in the pond. On the 12th of last month (June 1938) a lab. boy brought me some weed which I had placed in the water and on the 13th there were eggs! The male was still on land, but one presumes that, either he went in the water for a time or the female came out for him.'

Finally, long after the completion of the investigations dealt with in this paper, there came to my notice an account by Van Nieuwenhoven & Lever (1946) of similar work carried out in Holland during the war. The Dutch workers found snails of the genus *Limnaea* kept in aquaria without water plants and fed regularly on lettuce reacted to the addition of water plants by producing eggs within a few hours.

In the account that follows I give the results of experiments designed to test the importance of

vegetation and associated factors on the reproduction of newts. These experiments were carried out in 1936 and 1938 at Roman Hill Boys' School, Lowestoft, and they were only made possible by the help and close co-operation of the Headmaster, Mr W. H. Bleby, and two members of his staff, Mr Railston, in 1936 and Mr Bentley in 1938. In addition, I include some experiments on a smaller scale which I made in 1937. I have also to thank Dr E. S. Russell, Dr J. P. Harding, and Dr C. F. A. Pantin for reading through the paper and for helpful suggestions in interpreting the results.

EXPERIMENTS WITH NEWTS

(1) 1936

In planning the experiments of 1936 the aim was to test the hypothesis that the proximity of living aquatic vegetation would stimulate reproduction in newts and that this stimulus was not merely the mechanical convenience of water-weed as a bearer of eggs. To this end, new communities were established in the presence of both living and dead weed.

Conditions of the experiment.

Sixty newts were obtained from five neighbouring sources in north-east Suffolk in the last week of May 1936 (the breeding season in this district appears to have been delayed by the cold spring). From these were selected twenty-four specimens of *Molge cristata* Boulenger and twenty-four of *M. vulgaris* L., all showing good condition and maturity by their marked sexual dimorphism. For each species there were eight males and sixteen females.

One male and two females of the same species were put into each of sixteen tanks, eight for each species. The tanks were divided into two groups of eight, each group containing four tanks for each species. The tanks of the first group were numbered A1-A8 and those of the second B1-B8.

The tanks were rectangular, of clear glass and measured approximately 7 × 6 × 4 in. Each was filled to within 1 in. of the top with pond water. A quantity of the pond weed *Elodea canadensis* was obtained from the same source. This was carefully washed and then divided into two parts. The first was untreated. The second was placed in water kept at boiling-point for 15 min. After this treatment the difference in appearance between the two parts was

not noticeable but the boiled weed was more flaccid. Four 6 in. pieces of the untreated weed were placed in each of the group A tanks and the same number of 6 in. pieces of boiled weed were placed in the tanks of group B.

The tanks of both groups were set in alternate positions at a long window facing south. Gentle aeration was provided for each tank and the temperatures which were taken from time to time during the experiment showed a range of 55–72° F.

Insect larvae, tadpoles and fresh-water shrimps were placed in the tanks twice a week. Each tank received approximately the same amount of food.

To maintain constant daytime observation sixteen senior schoolboys were divided into morning and afternoon watches. Each boy was responsible for two tanks. They observed the number of eggs deposited, the mode of deposition, and the general behaviour of the subjects. A report under these three heads was made after each period of observation.

Results

In the tanks of group A containing live *Elodea* twenty-two eggs were laid. They occurred in five of the tanks and in each case were deposited on plant stems. Eight of the eggs were produced by *Molge cristata* and fourteen by *M. vulgaris*. The actual deposition of fifteen of the eggs was reported to have been seen by the watchers. Ten of the eggs were fertile and hatched out in from nineteen to 21 days after deposition.

No eggs were laid in the tanks of group B which contained boiled weed. The reports of the watchers of this group were verified by careful examination of each tank of the group at the end of the experiment.

Differences of behaviour were noted between the occupants of the two groups of tanks. Those in the tanks containing live *Elodea* showed the habit common to newts of basking on the surface of the water in sunny weather. At other times they were active in swimming. The males would frequently swim on their sides and rub the females with their crests. On the other hand, those in the tanks containing dead *Elodea* were more retiring and less active. They remained in the shade on sunny days and were more readily disturbed by external movements, than those of the other group. The males showed little attention to the females.

(2) 1937

On 12 April a small experiment was started with newts in two gold-fish bowls in order to see whether eggs would be deposited in water not containing weed. The result and an incidental circumstance are thought worth setting out in this place.

Conditions of the experiment

I found it difficult to obtain newts, and in two large gold-fish bowls containing only Lowestoft tap water I had to be content with one young *Molge cristata*, two male and one female *M. vulgaris* in bowl A, and two male and two female *M. vulgaris* in bowl B. The bowls were covered with flat pieces of glass and stood outside the south wall of a house in north Lowestoft where they were shaded by a box standing on its side. They were brought indoors on 18 April and placed on the ledge of a well-lighted window facing south.

Results

The observations made in the period 12 April–2 May are given below:

Date	Bowl A	Bowl B
16 April	<i>M. cristata</i> dead—removed	.
18 April	Water changed	Water changed. Slight growth of green algae. Nine eggs
19 April	Four eggs	.
23 April	Green algal incrustation on side of bowl	Green algal incrustation on side of bowl. One egg
24 April	.	Three eggs
25 April	.	One egg
2 May	Growth of green algae less than in B	Heavy growth of green algae. One egg

It is clear from this record that newts will deposit eggs in water which contains no weed. The two female *M. vulgaris* in bowl B deposited fourteen eggs, the one in bowl A, four only. In this connexion it may be noted that green algae were found in both bowls, but that there was a more profuse growth in the bowl in which occurred the largest number of eggs per female newt.

(3) 1938

In 1938 it was thought desirable to repeat the observations on the effects of live and dead plants on the deposition of ova by female newts and also to try some new tests. It appeared possible that the deposition of eggs in the tanks with boiled weed may have been inhibited by the products of decomposition of the dead weed rather than by the lower oxygen content and that the stimulus for egg laying was partly due to the presence of a suitable leaf or leaf-like shape in which the eggs could be wrapped. With these aims in view experiments were set up with living and dead weed and with artificial water plants oxygenated and not oxygenated. For each series of experiments, I also decided to have dark controls in order to exclude possible photometabolic effects.

Conditions of the experiment

Twenty-eight large gold-fish bowls each containing one male and two females of the common newt *M. vulgaris* were divided into four groups—A, B, C, and D—each consisting of seven bowls numbered one to seven. Groups A and B contained artificial pond-weed made from green oiled silk. Nine-inch strips of this material about 1 in. wide were cut comb-fashion and twisted. They were then fixed to porous pot ‘sinks’ with rubber bands and boiled. The bowls of group A had oxygen bubbled through the water for 2 hr. each day—1 hr. in the morning and 1 hr. in the afternoon. The oxygen was introduced through ‘mist’ aerators. Group B received no oxygen. Groups C and D contained *Elodea*, alive in group C and boiled in group D. Unfortunately it appeared during the course of the experiment that some portions of the *Elodea* had not been killed in the bowls of group D. Bowls 6 and 7 in each group were kept in darkness.

The newts were watched through the day by relays of boys. Eight boys were on duty at a time—two boys for each group. The boys worked in relays and were relieved every hour. They made notes on the behaviour of the newts and the deposition of eggs.

Small earthworms were fed to the newts every 2 days and untouched food was removed.

Results

A record of the appearance and number of eggs is given in Table 1. It will be seen that the largest number—twenty—was found in the bowls containing

normal live *Elodea* and that in the group containing boiled *Elodea* there was the smallest number—one. While in 1936 no eggs were found in the boiled *Elodea* experiments, in 1938 it appeared that parts of the *Elodea* had not been killed and if egg-laying is connected with the photometabolism of this water plant, the appearance of the single egg would be explicable.

Fifteen and seven eggs were found in the groups containing oxygenated and non-oxygenated artificial weed respectively. While the bubbling of oxygen has not resulted in as many eggs as the live *Elodea* series, it is notable that more eggs occurred in the non-oxygenated artificial weed bowls than in the boiled weed group. Of the eggs that occurred in the two most productive groups only nine out of twenty were observed to have been deposited on the live *Elodea* leaves, and two out of the fifteen on the ‘weed’ of the oxygenated artificial weed.

- These observations suggest three inferences.
- (1) That the presence of oxygen as supplied is an important effective agent in bringing about the deposition of eggs, but that this was not as effective as live *Elodea*.
 - (2) That killed or partly killed *Elodea* suppresses egg-laying.
 - (3) That the presence of the leaf of a water plant or similar object is not of prime importance for the production of eggs.

Of the bowls kept in darkness, eggs were only deposited in the series containing artificial weed and supplied with oxygen. It is clear therefore that,

Table 1. Investigations into the conditions influencing the breeding of newts, May 1938. Records of eggs

Date	Artificial pond-weed (X)														Total for day (X)	<i>Elodea</i> (Y)														Total for day (Y)	Total X+Y						
	A. Oxygenated							B. Not oxygenated								C. Alive							D. Boiled														
	1	2	3	4	5	6	7	1	2	3	4	5	6	7		1	2	3	4	5	6	7	1	2	3	4	5	6	7								
May 16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1							
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22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1								
23	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	2								
24	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	2								
26	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	1	3	1	.	.	.	.	.	.	.	.	.	5	7								
27	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	.	.	3	4								
28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	—	—								
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30	.	.	.	1	1	1	1	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	3	7								
31	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	3	4								
	1	4	1	3	2	3	1	—	3	3	1	—	—	—	6	4	5	3	2	—	—	1	—	—	—	—	—	—	—								
Totals	15							7							22							20							1							21	43

N.B. Jars 6 and 7 in each case were in the dark. Nine eggs in group C were deposited on weed. Two eggs in group A were on the weed.

either directly or indirectly, oxygen alone can bring about egg-laying.

The superiority of live *Elodea* to bubbled oxygen deserves further experimental attention with a view to finding out whether the difference was due to the time, rate or quantity of oxygen resulting from photosynthesis or to some other metabolic effluent of the plants. Information on this question could be obtained by varying the oxygen supply to series of artificial weed communities.

There are certain general observations on the behaviour of the newts in the four groups which are worthy of record. First of all it can be said that the newts in the bowls of boiled weed were the most unhappy; throughout the period of the investigation they were lethargic and were observed attempting to leave the bowls. They shed their skins and the males lost their crests. In the artificial weed series the animals were fairly lively for the first 4 days and although there was some skin shedding, eggs were laid. During the remainder of the period they were extremely lethargic and no more eggs were laid. They frequently attempted to leave the bowls and nearly all shed their skins. The newts in the live weed and oxygenated artificial weed series became more lethargic towards the end of the period but eggs were being laid throughout. In the live-weed series skins were being lost on the sixth and seventh day and the crests of males that had begun to disappear on the twelfth and thirteenth days had disappeared on the fifteenth. No cast skins or lost crests were reported from the series supplied with oxygen and it is clear that this difference in behaviour will have to be confirmed and investigated in subsequent work.

DISCUSSION

The general inference from these experiments is that, of the factors which make the presence of the water-weed *Elodea* a cause of egg deposition in newts, the production of oxygen is the most important. This, I think, is proved by the fact that no eggs were produced in conjunction with live *Elodea* in the dark, but that deposition occurred in the dark experiments with artificial *Elodea* and oxygen. While the oxygenated artificial *Elodea* experiments did not result in so many newt eggs as the live *Elodea*, it is possible that either the experimentally supplied oxygen was not given in such quantities or concentrations as were supplied by the plant or that some other substance may have had an additional positive effect. If so, it seems clear that the substance must resemble the oxygen of photosynthesis in being produced only in the presence of light. Finally we have to bear in mind as a possibility that egg deposition may be produced by low carbon-dioxide tensions resulting from the supply of oxygen.

The experiences of Nieuwenhoven & Lever with

Limnaea were similar to mine in some respects. They found that eggs were produced when the snails had been allowed to come into contact with the leaves of *Hydrocharis*, but not if the weed was separated from the snail, or dried, or kept in the dark. The reaction was also produced when the snails were introduced into the water that had been rendered rich in oxygen beforehand by passing pure oxygen through it, but not by passing oxygen over or through the water in which the snails were present or by a gradual increase in oxygen content, or by brief exposure to pure oxygen. On the other hand, *Elodea* had no effect even with extra illumination.

The Dutch investigators conclude that, as *Elodea* does not produce any response, oxygen is not the only effector of the egg-laying reaction. However, in view of the differing reaction to the supply of oxygen shown in these experiments, it may be that the difference in rate of supply or concentration of oxygen might account for the various responses and that the snails might have some specific response range in regard to oxygen which would not be filled by a plant like *Elodea* for instance. If this is true, it would not be necessary to postulate some special substance, although the point I have already mentioned about carbon dioxide tension would still be valid.

Apart from Dr Harding's observation on *Amblystoma*, cited at the beginning of this contribution, I do not know of any other instances in which the action of aquatic vegetation has been connected with the spawning of Amphibia. There should be a plentiful material among fish for experiments on the lines just undertaken and I look forward to an extension of our knowledge of general ecology in this physiological aspect. It is clear that one of the next steps to take in connexion with such work will be the arrangement of experimental series in which the rate of supply and concentration of oxygen is known and in which the carbon dioxide tension is simultaneously determined.

SUMMARY

1. In 1936 experiments were set up using twenty-four individuals each of the newts *Molge cristata* and *M. vulgaris* in the presence and absence of the pond weed *Elodea canadensis*. Twenty-two eggs were laid in the tanks with water weed, none in those without.

2. Of two bowls containing *Molge vulgaris* females and males in the spring of 1937 eggs first appeared in the bowl in which green algae first appeared.

3. Four sets of seven gold-fish bowls containing two females and one male of *M. vulgaris* were set up in 1938. One set was bubbled with oxygen, the second was without, the third contained *Elodea* alone and the fourth dead *Elodea*. Most eggs occurred in

reaches of the estuary and the river confined more to the Welsh side.

The encroachment of the land into the estuary is thus to a large extent artificial and of economic value in that the large area of reclaimed land forming Sea-land is now used for crop-growing and is suitable for human habitation, while Burton marshes are suitable for sheep and cattle grazing. The economic value of the estuary as a port has, however, deteriorated since the end of the nineteenth century.

In 1810 there was a deep L.W. channel at Parkgate, the port of departure for Ireland; and even as recently as the 1914-18 war, the local fishermen recall mooring their boats opposite Parkgate where the channel was still deep at L.W. In 1946-7 the boats had to be moored lower down the estuary at Heswall, where the L.W. depth was *c.* 2 ft. and in 1948 they have moved down to Thurstaston.

About 80 years ago the spring tides flowed right up

to Shotwick, but at present it takes the spring tides to cover the estuary up to the edge of Denhall marshes, while during neap tides large areas of mud along from Gayton, Parkgate to Denhall remain exposed for several days. Similarly, on the Welsh side large mud banks remain exposed at neaps. Figs. 4-6 show that the immediate effect of reclaiming the land was the diversion of the main channel to the Welsh side in the upper reaches and then its swinging back to the Cheshire side beyond Burton. Thus the channel was no longer flowing directly seawards and many banks appeared in mid-estuary. This swinging of the channel (Dawpool Deep—Fig. 6) at the present time is endangering the Thurstaston-Gayton banks which receive the full force of the spring flood tides.

(b) *Other causes of change*

The first recorded changes in the estuary were produced artificially, but further and recent changes,

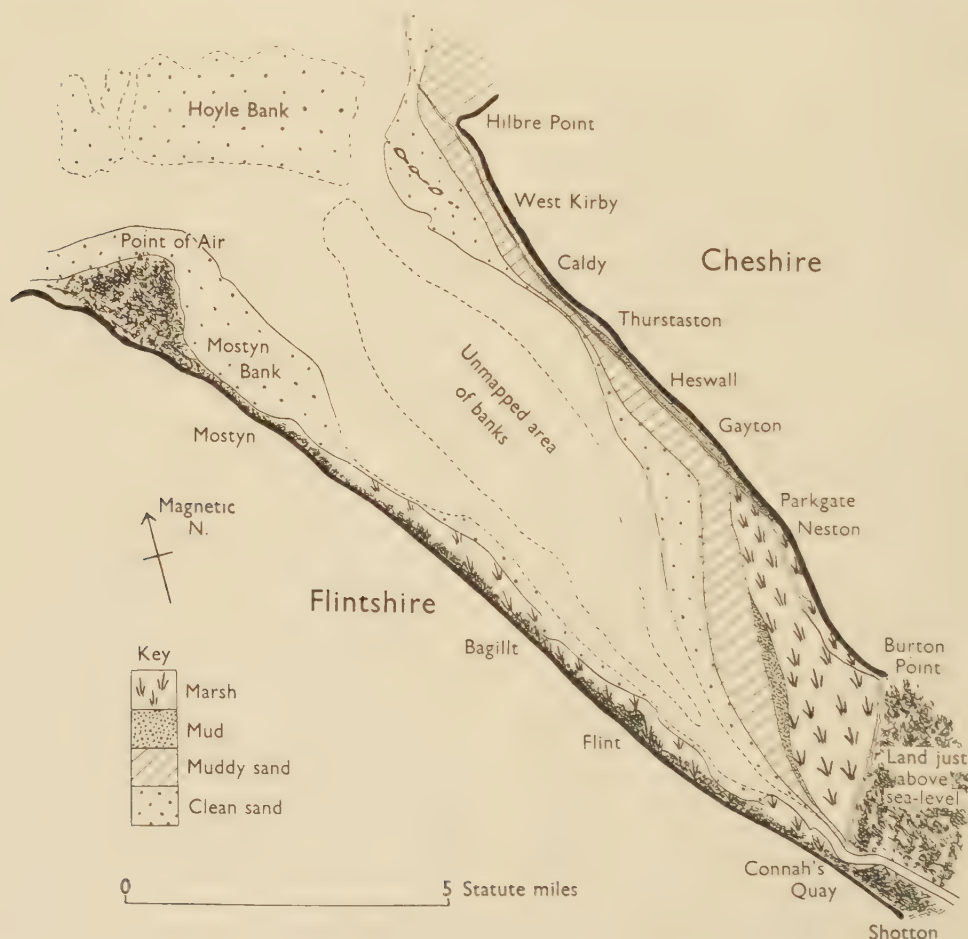


Fig. 1. Showing the general distribution of the types of substrate in the Dee Estuary, 1946-47.

when the encroachment has increased from the original banks towards mid-estuary, are due to the gradual raising of the river bed with the deposition of silt. It is calculated that organic matter equivalent to 100 tons of organic carbon is discharged into the Mersey each day. This is probably very much larger than that discharged into the Dee, where the main banks remain sandy. Some silt is probably carried down from the upper reaches of the River Dee but another portion, as in the River Mersey (D.S.I.R., 1938), is derived from erosion of boulder clay cliffs and from the bed of Liverpool Bay and the Irish Sea carried up with the tide.

The New Cut keeps the river flowing along its narrow channel with some force, but almost immediately the Cut ends, the estuary fans out to several times its previous width, thus decreasing the ebb force and causing the deposition of suspended matter. The force of the main channel prevents the laying down of much silt so that it is towards the banks, where the flow is relatively less, that there is most deposit. This soft silt is soon colonized by halophytes once it becomes exposed during low water. In this area *Salicornia stricta* (europea) gains the first foothold and the network of its roots assisted in the retention of more silt and sand, thus reducing the water content to give a stable substrate of muddy sand. Other halophytes, *Festuca ovina*, var. *maritima* and *Aster tripolium*, follow in the colonization and form a true salting. In this way the Neston and Parkgate marshes have spread towards mid-estuary and as far as Gayton within the last 2 or 3 years, and the process is continuing rapidly.

A different kind of encroachment is taking place at the mouth between West Kirby and Hoylake, where the substrate is sandy. Typical sand-dune vegetation—*Glaux maritima*, *Ammophila* (*Psamma*) *arenaria*—is colonizing from the golf dunes behind. At present, however, this process is slow and is apparently to be checked by the local authorities.

(c) Conditions in 1946-7

The Dee estuary covers a large area over 15 miles long and 4 miles wide. An ecological survey of the Cheshire foreshore from Burton Marshes to Hilbre Point was carried out from August 1946 to August 1947.

The general distribution of the types of substrate found in the estuary is shown in Fig. 1. The marshland extends from Burton to Gayton and serves as grazing land as far as the old Wirral colliery, where it is never completely submerged even by spring tides. After these tides, however, the water in the marsh takes several days to drain back into the estuary along deep narrow channels which have a salinity of approximately 25 ‰ at high tide. Except at the extreme edge

there is no *Salicornia*, the development of the marsh having advanced to make *Festuca ovina* var. *maritima* the dominant species. Subdominants are *Suaeda maritima* with a uniform distribution and *Obione portulacoides* which is confined to the borders of the gulleys. *Triglochin palustris* and *Aster tripolium* are fairly common, while *Arenaria peploides* is rather rare.

The grazing marsh thins out towards Neston and Parkgate as the level drops and the land is covered by the spring tides. *Salicornia* and occasional specimens of *Festuca* and *Atriplex* are the only species found beyond Parkgate.

The marshland extends about a mile towards the main channel at Parkgate and remains exposed for several days during neaps. It consists of numerous hillocks bearing mainly *Festuca ovina* with *Phragmites communis*, *Scirpus maritimus*, *Obione portulacoides*, *Suaeda maritima* and *Aster tripolium* fairly abundant and occasional specimens of *Triglochin palustris*, *Arenaria peploides* and *Plantago maritima*. Around the hillocks are 'pans' or shallow pools which have no macroflora. Towards mid-channel where the substrate changes from firm mud to muddy sand, the marsh thins out and is bordered by *Salicornia stricta*. The entire marsh is exposed at H.W.N.

The foreshore bordering Burton marsh is below H.W.N. and consists of soft mud deposited by the tide which is slack, owing to the widening of the estuary. A similar deposit occurs along the promenade wall from Parkgate to Caldy.

The substrate becomes progressively less muddy towards the main channel and mouth of the river until that bordering the main channel is 'clean' sand, golden in colour. Thus, silt is inversely proportional to tide level and therefore tidal force. Except where the substrate is bound by roots, the tide, which runs at about 5 knots, may cause shifting of the bottom deposit varying from local deposits of mud in slack regions to shifting of whole sandbanks.

Almost the entire estuary remains exposed until about 2 hr. before high tide, because the river bed is at a high tidal level.

2. FACTORS AFFECTING THE PRESENCE AND DISTRIBUTION OF SPECIES

As in most estuaries, the fauna of the Dee estuary is limited in species although actual individuals are very numerous. The factors affecting the fauna in the Dee are:

(a) Salinity

The mixing of sea water with fresh water from the river reduces the salinity and thus limits truly marine species, while the variation in salinity due to periodic

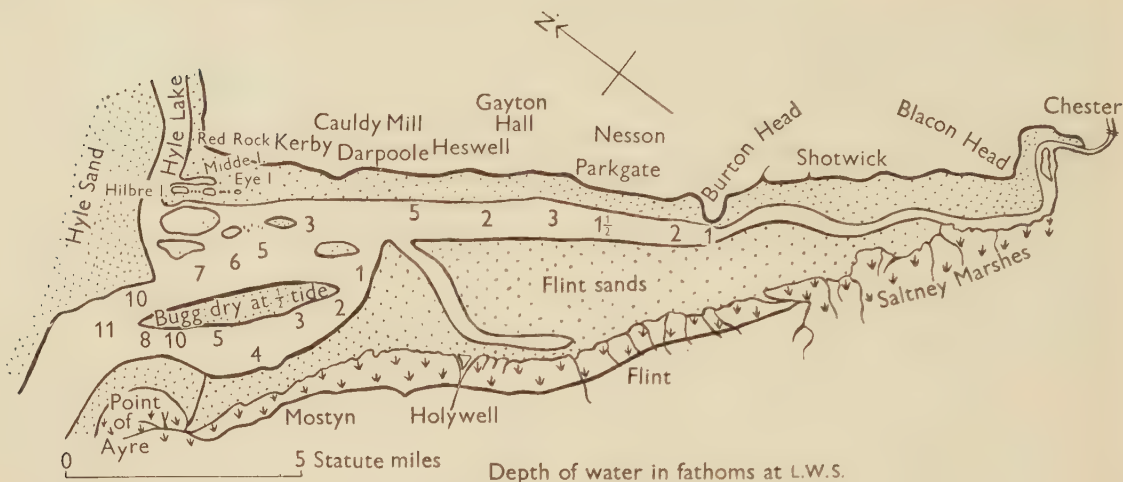


Fig. 2. 1684 Dee estuary.

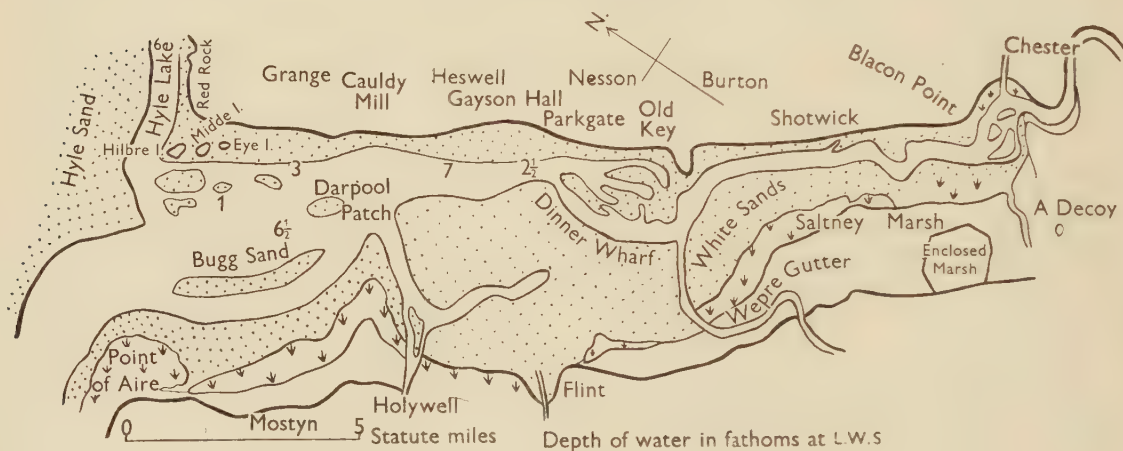


Fig. 3. 1732 Dee estuary.

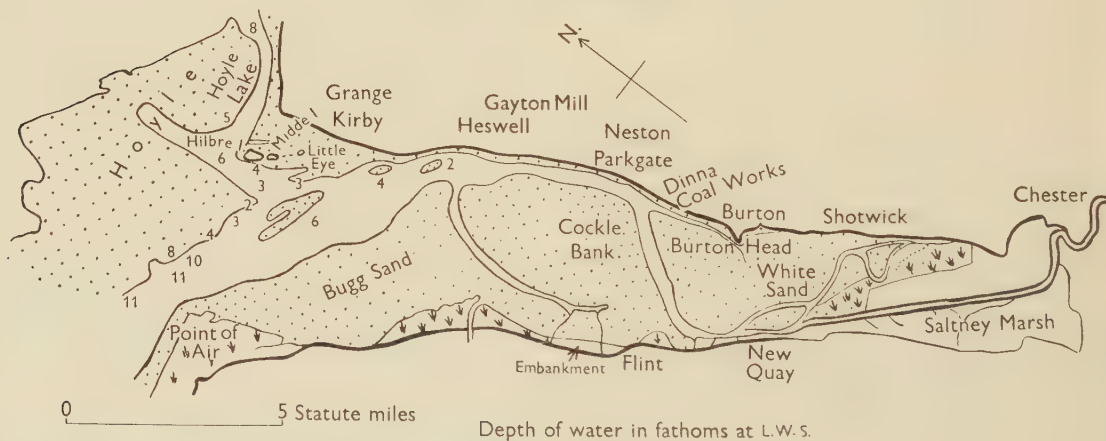


Fig. 4. 1771 Dee estuary.

mixing, limits the species further. As a consequence of the high tidal level of the exposed part of the estuary, the ebb tide persists for nearly 10 hr. so that the change of salinity is rapid during the 2 hr. flood tide. The salinity of the main estuarine channel at L.W. is between 20 and 30‰, but in the smaller channels the fresh-water drainage from the banks lowers the salinity to about 15‰ and in heavy rain or thaw it

great and the flood tide has lost its strength so that at Queensferry and Chester the salinity is almost negligible at any state of the tide. Water samples were taken from the surface metre only and, since the D.S.I.R. report (1938) on the Mersey shows that there is efficient mixing in a shallow estuary, no allowance was made for the lack of mixing of fresh and sea water due to variation in their specific gravities.

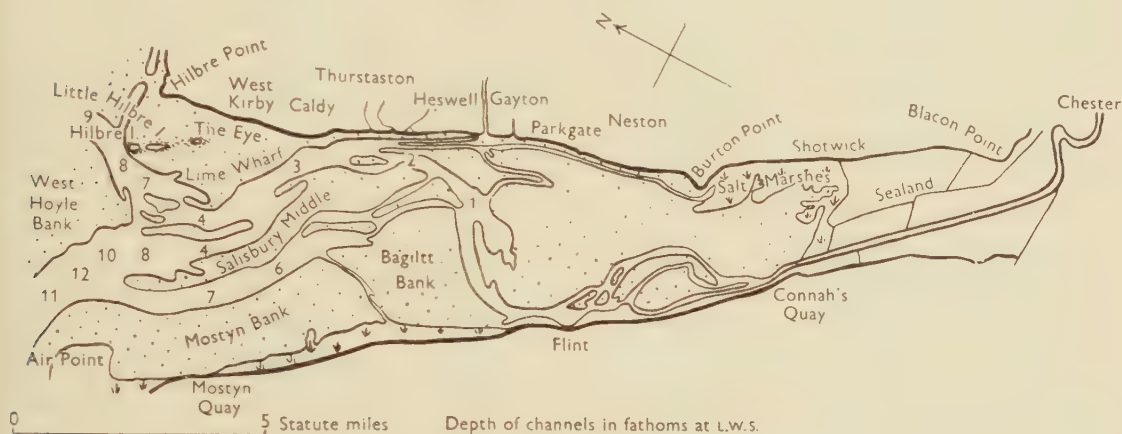


Fig. 5. 1839 Dee estuary.

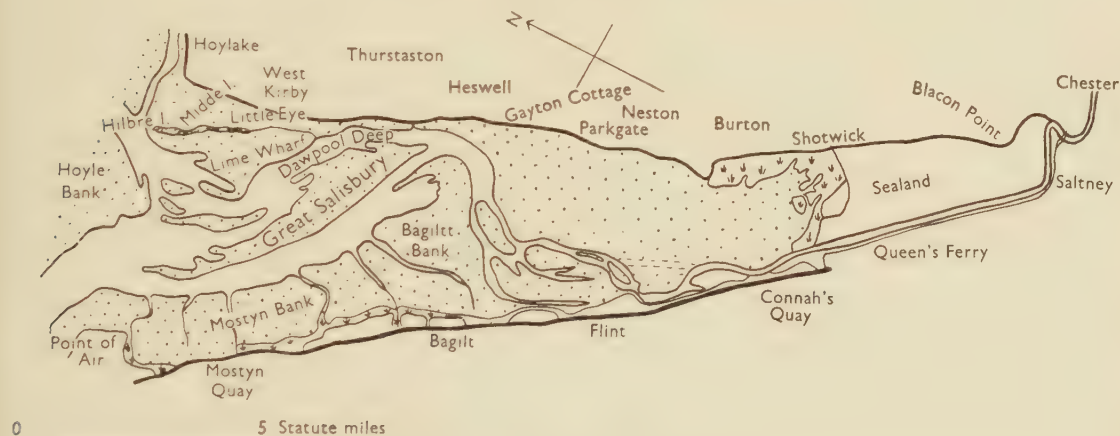


Fig. 6. Feb. 1849 Dee estuary.

may be reduced to less than 1‰. The sea beyond the estuary has a salinity of about 33‰ and at high tide the main estuary water may be raised to 30‰. The decrease in salinity from the mouth up the estuary is shown in the series of samples taken as near the same date as possible at low and high water from Hilbre Island up to Chester (Table 1). From Hilbre to Parkgate where the estuary is wide, the decrease is small as there is a large volume of sea water; but in the New Cut the volume of fresh water is comparatively

Samples taken in various localities throughout the year indicated that the salinity is greatest in late summer and autumn and least in early spring. (N.B. There was a heavy thaw in March-April 1947.) In occasional samples of interstitial water in the sand and mud, tested for salinity, it was found that the salinity was higher than in the neighbouring channels at L.W., the difference being as much as 10–20‰ (Table 2). Thus the salinity of the substrate water, while subject to change, is much less variable than the

Table 1. *Increase of salinity towards the mouth of the river (Hilbre)*

Main Channel at L.W.			
Place	Date	Tide	Salinity (‰)
Chester	14 Oct. 46	L.W.S.	0.33
Chester	3 Nov. 46	L.W.N.	0.31
Queensferry	14 Oct. 46	L.W.S.	0.974
Queensferry	3 Nov. 46	L.W.N.	0.647
Parkgate	18 Nov. 46	L.W.	20.83
Parkgate	18 Apr. 47	L.W.	15.73 (thaw)
Gayton	20 Jan. 47	L.W.	22.12
Gayton	15 Apr. 47	L.W.	14.11
Heswall	10 June 47	L.W.	29.8
Caldy	19 May 47	L.W.	25.6
Hilbre	17 Dec. 46	L.W.	26.85
Hilbre	29 May 47	L.W.	29.4
Main channel at H.W.			
Chester	13 Oct. 46	H.W.S.	2.41
Chester	2 Nov. 46	H.W.N.	0.93
Queensferry	13 Oct. 46	H.W.S.	2.48
Queensferry	2 Nov. 46	H.W.N.	1.02
Denhall	17 Sept. 47	H.W.S.	30.2 (equinox)
R.B.H.	25 Oct. 46	H.W.S.	30.79
R.B.H. I	27 Sept. 46	4 hr. flood	28.55
R.B.H. II	27 Sept. 46	4½ hr. flood	27.38
R.B.H. III	27 Sept. 46	5 hr. flood	23.57

R.B.H. = Red Buoy Hollow, the samples being taken from a boat.

Narrow channel at L.W.

(Visible from H.W.N. to L.W. from Parkgate to Hilbre Point)

Place	Date	Salinity (‰)
Parkgate	8 Dec. 46	18.1
Parkgate	18 Apr. 47	0.171 (thaw)
Parkgate	19 June 47	12.8
Gayton	20 Jan. 47	3.845
Gayton	15 Apr. 47	0.98 (thaw)
Heswall	26 June 47	28.0
Caldy	19 May 47	25.6 (high temperature)
Caldy	20 May 47	30.2
Hilbre	27 May 47	31.6

Table 2. *Interstitial water of the substrate*

Place	Stn.	Type	Date (1947)	Salinity (‰)	Nearest free water	Salinity (‰)
Parkgate	'6'	Clean sand	25 Apr.	26.0 (thaw)	Main channel	15.73
Parkgate	'6'	Clean sand	8 July	27.0	Pool water '4'	31.8
Heswall	'4'	Clean sand	26 June	31.0		
Thurstaston	'2'	Mud	17 Apr.	28.64 (thaw)	Main channel	18.26
Thurstaston	'1'	Sand	17 Apr.	1.41 (thaw)	Main channel	18.26
Hilbre	'4'	Sand	30 June	32.2	Main channel	30.82
Hilbre	'6'	Sand	30 June	33.8	Main channel	30.82

While the salinity of the free sea water is greatly altered by thaw and drainage and evaporation, during hot weather the interstitial water remains more constant. The numbers in inverted commas indicate the particular station in the sector (Map 2).

free overlying water—a point of importance to burrowing animals.

(b) Exposure

Since the flood tide lasts only about 2 hr. the foreshore is covered for about 4 hr. per tide. The region between H.W.N. and H.W.S. is uncovered for several days at neaps, and this flat unsheltered area which stretches for several miles may be exposed to high winds, strong light, variations in temperature, and to predatory animals—man and birds—and may lack food from the sea in the form of plankton and detritus. There are very few rocks or pools left as shelter on the foreshore and the only protection is afforded by the marsh flora.

(c) Silt content and water content

These factors are interdependent. Experiments were carried out, by drying samples of known weight, to find the water content of the substrate in various regions. Samples were obtained with a wide glass tube open at both ends, and the top 2 cm. layer was cut off for comparison with the rest of the sample. In a similar manner, samples were taken for silt analysis. The dry weight of the samples was found and they were stirred with distilled water and the silt decanted off after standing for 5 min.

Samples of the three typical types of substrate throughout the estuary—mud, muddy sand and clean sand—are seen in a sector from H.W. at Parkgate to mid-estuary (Figs. 7 and 8). The types are distinguishable by colour: the mud, having a high percentage (10–15 % of dry weight) of silt, is black, the muddy sand is browner since the silt content is lower (1–3 % of dry weight), while the clean sand is 'golden' and is almost devoid of silt. Samples taken from Caldy for comparison gave similar results. The results show that the water content of the substrate varies with the silt content, being highest in mud and lowest in sand. This is to be expected since texture and size of particles play an important part in water retentive capacity.

In general the percentage of silt is somewhat lower in the upper 2 cm. owing possibly to its removal in suspension by the overlying sea, since the silt content varies according to the state of the tide. At neap tides when the flow of the water is gentler, the silt content is more than twice the amount in similar mud at spring tide, particularly in regions about H.W.N. line, where the mud is only just covered by the neap tide.

The samples were taken as nearly as possible to L.W. time (Tide Datum), so that the mud samples from near H.W.M. had been exposed for at least 6 hr. and at neaps for up to 10 days. Hence in the experiment the actual water content of the substrates under

normal conditions was compared and not their water retentive power.

In *mud* the water content may be over 40 % of the dry weight after spring tides, and in autumn, winter and spring, even during neap tides after several days' exposure, the water content may be 35 % of dry weight. The water level is kept up by capillarity from the lower layers and is maintained by rainfall and high humidity which retards evaporation from the surface.

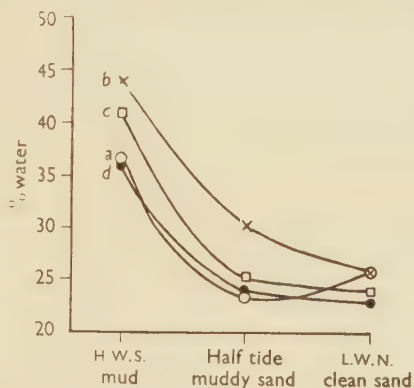


Fig. 7. Parkgate water content. Percentage of water in top 2 cm. layer. *a*=Neaps, winter, *b*=Springs, winter, *c*=Springs, summer, *d*=Neaps, summer.

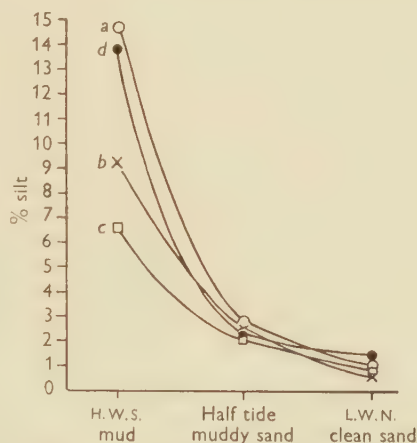


Fig. 8. Parkgate silt content. Percentage of dry wt. in top 2 cm. layer. *a*=Neaps, winter, *b*=Springs, winter, *c*=Springs, summer, *d*=Neaps, summer.

In the summer of 1947, weeks without rain and an air temperature of 70–80° F. caused a drying up and caking of the surface mud when the water content sank to 5 % in the surface 2 cm. This layer formed a protective crust over the rest of the mud by preventing further evaporation so that the water content remained at 15 % and the mud was habitable for burrowing forms.

The *muddy sand* areas are found towards mid-tide level at Parkgate between the marsh and clean sand. Towards the mouth of the estuary the area becomes wider, reaching both a higher and a lower tidal level. The silt content is never more than 5% of the dry weight and the water content is between 20 and 30%. As in the mud, the silt content of the surface is less than that of the lower layers.

Clean sand is found near the clay banks at H.W.S. at Heswall and Thurstaston, near the mouth of the estuary and bordering the main channel. In the latter regions the water content is *c.* 25%, since it is near L.W.M. and there is little exposure and drainage, while at high tide levels there may be less than 5%. The silt content is almost negligible.

(d) *Texture*

In all types of substrate the sand is very fine, most of it passing through a 0.5 mm. sieve, and is thus suitable for burrowing animals. In areas by the main channels and beyond Hilbre Island broken shells form a fine gravel. Along the banks from Gayton to Caldy, there is a narrow strip of stony substrate, too coarse for burrowing forms. It also appeared to be devoid of such forms as *Orchestia*, possibly because of the lack of either living or decaying flora.

Seasonal examination of sectors along the north-east shore shows that while the distribution described above is fairly constant, individual variations occur. As previously mentioned, silt may be washed out to some extent during spring tides; similarly, sand is washed on to mud regions, either forming a surface layer or becoming well mixed; and whole sandbanks may be shifted. A notable variation occurs towards the end of spring and beginning of summer when large areas normally covered with sand or muddy sand become covered with a layer of mud which varies in depth from 1 to 20–30 cm. This seemed to be due to suspended matter falling as temporary mud deposits, partly because of the creation of slack and back waters during the less active summer tides and partly because of the higher proportion of suspended matter in the form of moribund plankton, faeces, food and larval forms, etc. Towards the middle of August most of these deposits had disappeared. They were not observed during the previous autumn and winter (1946), and as similar deposits have been recorded previously (Orton, 1937), their disappearance is probably seasonal.

(e) *Pollution*

Pollution may be a major factor in an estuary—e.g. in the Mersey (D.S.I.R., 1938) it is calculated that 1000 million gallons of sewage and industrial effluents are discharged into the estuary per day and shipping may cause oily films on the mud when the tide recedes.

In the Dee there is no significant amount of shipping, though there are large chemical and textile works along the Welsh bank. The main local effects on the Cheshire shore are due to sewage effluents. Sewage from some of the houses opens directly into the narrow channel at Parkgate, thus affecting the neighbouring mud. From the Heswall sewage works, operating only at high tide, the effluent is piped out as far as the muddy sand region, nevertheless, the Lancashire and Western Sea Fishery Board state that cockles and mussels collected in the area are unfit for human consumption. In 1933 Orton (1933*b*) observed *Arenicola* dying in large numbers and found that it was due to a bacterium affecting the gills; there was also a high mortality of adult *Cardium edule* (Orton, 1933*c*). These observations occurred during a warm summer which would help to increase the effect of pollution. Nevertheless, young fish were apparently quite healthy in the nearby channels and in spring 1947 hundreds of living 1 in. flatfish were observed in the Parkgate drainage channel. Pollution in the Dee therefore, while it no doubt limits the occurrence of species, does not have any ill effects on the normal population except during a warm summer.

3. METHODS

Collecting was done on transects at Hilbre Point, Caldy, Thurstaston, Heswall, Gayton and Parkgate. In addition to a general survey of the fauna in the area, three main sections were selected from high water at Parkgate, Heswall and Hoyslake respectively to the main channel, and stations were chosen at different tide levels and in different types of substrate for seasonal study. This was done quantitatively by measuring a $\frac{1}{4}$ sq.m. with a wooden frame, counting the enclosed surface fauna and then digging rapidly to a depth of 10–20 cm. and sieving the entire volume through a 1.0 or 0.5 mm. sieve with water from the neighbouring pools or channels. Animals left in the sieve were then counted, care being taken to count only the heads of worms, which were liable to get broken during the process.

A prismatic compass was used to note the positions of the stations, areas and tidal levels. The so-called main channel in this work drains the Cheshire side of the estuary and was used as a limiting line, as it is roughly mid-estuarine and too deep to cross on foot. The shipping channel lies along the Welsh coast south-west of this.

4. GENERAL DISTRIBUTION OF THE FAUNA

The fauna may be briefly classified into surface and burrowing forms.

(a) *Surface forms*

These have little protection on this type of foreshore.

(i) *In marsh areas*

The flora affords protection for many types of arthropods, the commonest of which are Diptera and other winged insects—skaters (*Gerris* sp.), aphids, the collembolan *Archisotoma besselsi* (Packard), a small black spider and various marine mites.

It is not exposure that these air-breathing arthropods have to combat, but periodic submersion, for a few days each fortnight, by the spring tides. Diptera and other winged insects no doubt escape to the neighbouring land, but the wingless forms remain. Immersing the latter overnight in screw-top jars filled with sea-water, proved that aphids survived if a tuft of *Festuca* was placed in the jar and they were able to crawl between the folded leaves. The spiders probably obtained similar protection from the base of the leaves. The Collembola survived because an envelope of air was retained round each animal, even when the jar was shaken violently. In the field it is possible that they burrow into the sand as the tide comes up. That they burrow to lay eggs is probable, since on digging to 10–20 cm. in the sandy soil at Parkgate, many groups of eggs were found in September. Samples brought back to the laboratory did not hatch, but in the same region in the following March, white exuviae of Collembola were found among batches of eggs, suggesting that they had been hatched from the eggs and moulted before escaping to the surface. (The survival of submerged intertidal insects is discussed by Brown (1948) in connexion with saldid bugs in salt-marshes.)

(ii) *Unsheltered areas*

The remaining surface animals are truly aquatic and have become adapted to varying amounts of exposure. The only two surface dwellers found to any extent in the estuary are shore crabs (*Carcinus maenas*) and snails (*Hydrobia ulvae*). The former is well adapted to exposure and changes in salinity. Specimens found in mud and muddy sand are small (5–10 mm. carapace width) but the pools contain a few measuring 20–30 mm. All specimens have blunt projections rather than teeth on the anterior edge of the carapace, which is variously coloured, sometimes with marble markings, sometimes plain olive green and sometimes with an orange stripe. They were much more abundant in summer, when three to four small crabs were found per sq.m. of ground. They often found protection in the hole formed in the sand by a *Mya* siphon. There seems to be no dwarfing of forms such as is found in the Mersey (Fraser, 1932) and large *Carcinus* are fairly numerous in the deep channel of the Dee

where they are caught in the shrimp nets. They were absent from the foreshore, evidently because it offered them no protection.

Hydrobia ulvae was more abundant and widespread than *Carcinus maenas*. In muddy inshore regions in September and October 1946, it formed almost a complete covering, numbering about 12,500 per sq.m. of surface area. The numbers increased in shallow pools but decreased on muddy sand, while towards the main channel in the clean sand there were only about 12 per sq.m. Before the end of December, however, almost all the *Hydrobia* had disappeared. Undoubtedly large numbers died, for there was an increased number of dead, empty shells in the mud sievings. Few living specimens were found on sieving but it is possible that many small ones escaped detection by passing through the sieve. The sudden reduction was not due to the severe winter, which did not start until a month later. This almost total absence of *Hydrobia* persisted until June–July 1947, when numbers were again seen on the surface, though up to the end of August 1947, when observations ceased, there were never as many as in 1946. This evidence suggests that *Hydrobia* is an annual, the adults dying off while the young ones spend the winter burrowed in the substrate, ready to form the next summer population. Further observations would be necessary to support this suggestion, but the mortality may not be annual and may have been due to adverse conditions which particularly affected *H. ulvae* since no similar mortality was observed in other species.

Hydrobia appears to have a water preference, probably correlated with its habit of feeding on detritus, as it tends to accumulate in the 'pans' and damper areas. On the other hand, it is found near H.W.S. where it is exposed for several days. The reactions of *Hydrobia* to immersion seem to vary. Lambert (1930) remarks that this species, while surviving in putrid mud, has a definite objection to continuous immersion and if immersed in stagnant water will crawl out and die. The accumulation in 'pans' at Parkgate would therefore appear to be a temporary population. In the laboratory *Hydrobia* crawled out of dishes of sea water, but when this was diluted to one-third of its salinity, it remained indefinitely immersed. Hence, salinity rather than length of time of immersion may limit *Hydrobia* to higher tidal levels. On the other hand, McMillan (1941 a) records it as abundant on Hilbre Island where the salinity of the flood tide is 30‰ or more. It must be mentioned that the animals which remained indefinitely (7 weeks) immersed were carrying eggs and it may be that a change of habit occurs at this time, when it is advantageous in keeping the eggs moist and ensuring larval release in water. These varying results of the effect of submersion on *H. ulvae* suggest that

this form, which originally had a brackish water habitat, is in the transitional stage of osmo-regulation.

Experiments on numerous specimens collected after tidal immersion and kept in dry watch-glasses (room temperature 60–85° F.), showed that all individuals survived dry warm conditions (cf. summer shore) for 4 days, after which there was a gradual reduction of the percentage of survival, until only 15 % survived 2 weeks and all were dead after 17 days under these conditions (Fig. 9). In the field, conditions are rarely, if ever, as severe as in the experiment and the animals may burrow several cm. into the mud to avoid desiccation. Lack of food may be a secondary cause of death in the laboratory.

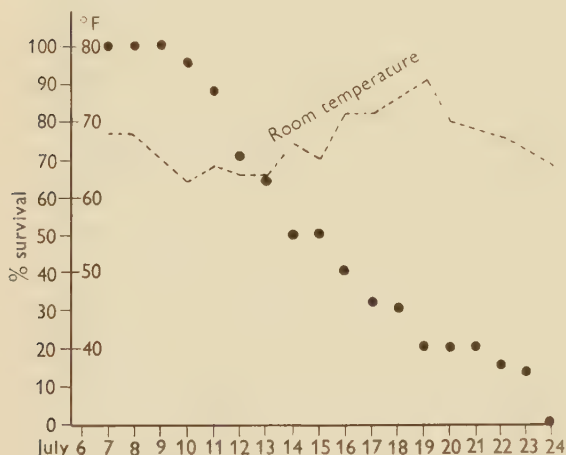


Fig. 9. *Hydrobia ulvae* survival. Temp. ----, % survival ●●●, plotted against time in days.

The only other surface forms were *Mytilus edulis* and *Littorina* spp. found locally on stones on Heswall and Gayton mud. *Macoma balthica* and *Cardium edule* are temporary surface dwellers. Exposure thus greatly limits the surface macrofauna of the estuary.

(iii) Pools and channels (Table 3)

Non-burrowing animals which are not adapted for surface exposure are limited to pools and channels left by the receding tide. Rocks are only found at Heswall, Caldy and Hilbre, where they are few and small. They serve as shelter for encrusting forms—Polyzoa, Hydrozoa, molluscs and the barnacles *Balanus balanoides* and *B. crenatus*.

Pools occur in the marsh, muddy sand and sand areas; but drainage and evaporation often cause their disappearance before the tide returns. Some of the larger pools in the sandy regions persist with a depth of 2 or 3 feet, and water remains in narrow drainage channels.

In the smaller pools the animals have to contend

Table 3. Fauna of pools in marsh, muddy sand and sand areas

CILIATA
HYDROIDA
<i>Obelia gelatinosa</i> (Pallas)
NEMATODA
NEMERTINI
<i>Lineus longissimus</i> (Gunnerus)
<i>Prostoma</i> (<i>Tetrastemma</i>) sp.
POLYCHAETA
<i>Nereis diversicolor</i> Müller
<i>Phyllodoce laminosa</i> (Gmelin)
OLIGOCHAETA
MOLLUSCA
<i>Cardium edule</i> L.
<i>Mytilus edulis</i> L.
<i>Macoma balthica</i> (L.)
<i>Hydrobia ulvae</i> (Pennant)
<i>Littorina littorea</i> (L.)
<i>Littorina rudis</i> (Maton)
CRUSTACEA
<i>Tigriopus fulvus</i> (Fischer)
<i>Balanus balanoides</i> (L.)
<i>Balanus crenatus</i> Bruguière
<i>Eurydice pulchra</i> Leach
<i>Sphaeroma rugicauda</i> Leach
<i>Gnathia maxillaris</i> (Montagu)
<i>Orchestia gammarella</i> (Pallas)
<i>Corophium volutator</i> (Pallas)
<i>Corophium arenarium</i> Crawford
<i>Hyperia galba</i> (Montagu)
<i>Carcinus maenas</i> (Pennant)
<i>Leander squilla</i> (L.)
<i>Crangon vulgaris</i> L.
ARANEIDA
COLLEMBOLA
<i>Archistoma besselsi</i> (Packard)
HEMIPTERA
Sp. of aphid
Channels
CRUSTACEA
<i>Janira maculosa</i> Leach
<i>Schistomysis spiritus</i> Norman
<i>Hemimysis</i> sp.
<i>Neomysis vulgaris</i> (Thompson)
<i>Crangon vulgaris</i> L.
<i>Carcinus maenas</i> (Pennant)
FISH
<i>Gobius minutus</i> Pallas
<i>Solea vulgaris</i> Quensel juv.
<i>Pleuronectes platessa</i> L. juv.

with: (a) Possible drying up. (b) Great variation in temperature and salinity of a small volume of water which will eventually mix with the flood tide. The temperature even in early spring may rise from 50 to 70° F. within a tide, and the salinity may vary from 15 to 32‰. (c) Reduction in oxygen content due to rapid rise in temperature.

Most pools have no flora other than diatoms, which

are very abundant in spring and summer, but occasional green algae (*Ulva*, *Enteromorpha*, and *Cladophora*) are found attached to rocks at Caldy and Hilbre. The pools in Denhall marsh contain halophytes. Some pool species, e.g. the amphipod *Orchestia gammarella*, unidentified spiders, *Carcinus maenas*, are normally not continuously immersed so that the disappearance of pool water has no adverse effect on them. Others survive by seeking protection from exposure by migrating into the underlying sand or mud (Crustacea, polychaetes, nematodes, lamellibranchs—*Cardium* and *Macoma*) or by contracting into their shells or protective envelope (gastropods, *Balanus* and *Obelia*).

Animals which cannot survive the drying up of pools are limited to the channels, where they are subject to a greater variation in salinity due to land drainage. Sessile Hydrozoa and sponges are rare or absent, probably because of lack of shells or stones for settling.

(b) Burrowing forms

Salinity, tide level, texture and oxygen content of the substrate are the controlling factors in the distribution of the burrowing fauna throughout the estuary. Table 2 shows that the salinity of the water retained by the substrate is not subject to such change as the overlying water and that on the whole it varies inversely with the tide level.

Texture is only a limiting factor along the stony Gayton-Caldy bank where burrowing fauna are absent, though bound up with texture is mud content and with this oxygen and water content. No actual oxygen measurements were made, but in the regions where the sand and mud, on disturbing, produced a strong odour of hydrogen sulphide, it was assumed that the oxygen was negligible or absent. The sand began to turn black about 15 cm. down, while there appeared to be no oxygen at 10 cm. or less in the mud.

(i) Fauna of mud

In the permanent mud along the bank from Parkgate to Caldy (Fig. 1) the salinity, except after heavy rain or thaw, is about 29‰. At Heswall and Gayton mud occurs below mid-tide level and remains waterlogged, but at Parkgate it is at about H.W.N. and is drier and more stable at low tide. The fauna is limited to the surface layers. The only animal burrowing below 10 cm. is the polychaete worm *Nereis diversicolor*, one of the most widespread species of the estuary. This and *Hydrobia ulvae* are the only macrofauna present in the mud at Parkgate. At Gayton and Heswall, where there is less pollution, other molluscs appear together with the amphipod *Corophium volutator*.

The mud was examined for microfauna by cutting

a sample from a glass tube of 3 cm. diameter, into 2 cm. lengths and examining drops of a suspension of each layer under the microscope. In this way a rough quantitative estimate of the microfauna at different levels in the mud was obtained (Table 4). Most of it occupies the top 4 cm. layer of mud and no fauna penetrates beyond 8 cm., probably because of the lack of oxygen and the compactness of the mud below this depth. Free-swimming forms—ciliates and *Amphiascus*—are presumably temporary mud dwellers, left by the receding tide. An extensive search was made throughout the year for *Protohydra* by bringing in quantities of mud, leaving them to settle in glass dishes and then examining the surface layer with a lens, but none was found.

Table 4. *Microfauna of Parkgate mud*

Depth from surface (cm.)	Fauna	Approx. number per c.c. suspension
2	PROTOZOA	
	<i>Loxophyllum</i> sp.	3
	<i>Acenita</i> sp.	5
	<i>Peritromus</i> sp.	2
	<i>Euplotes</i> sp.	15
	<i>Vorticellids</i>	20
	<i>Helicostoma</i> sp.	5
	FORAMINIFERA shells	15
	PLATYHELMINTHES	
	Turbellarians— <i>Provertex</i>	20
	NEMATODA 3 mm. long	50
	POLYCHAETA	
	<i>Clitellio</i> ?	1
	<i>Amphiglena mediterranea</i>	10
	CRUSTACEA	
	<i>Amphiascus</i> sp.	2
	<i>Tigriopus fulvus</i>	2
	<i>Calanus</i> sp.	1
	<i>Eurytemora hirundoides</i>	1
	MOLLUSCA	
	<i>Hydrobia ulvae</i>	12
4	NEMATODA 8 mm. long	10
	NEMATODA 5 mm.	50
	NEMATODA 3 mm.	20
6	ENCHYTRAEIDAE?	5
	NEMATODA 8 mm.	5
	ENCHYTRAEIDAE?	2
8	<i>Clitellio</i> ?	2
	NEMATODA 8 mm.	1
	<i>Clitellio</i> ?	1
10	No fauna	

At Gayton and Heswall, clumps of molluscs consisting of *Mytilus edulis*, together with a few *Littorina littorea*, *L. rudis*, *Hydrobia ulvae* and *Cardium* and *Macoma* valves, settled on small stones near the narrow drainage channel. *Scrobicularia plana* (da Costa), *Macoma balthica* and *Mya arenaria* are

found in the soft mud at different depths, the lower limit probably being controlled by the lengths of their siphons. *Scrobicularia plana* occurs generally in the top 4 cm. layer, often at least partially exposed since the specimens are small (c. 2 cm.). *Macoma balthica* is found at depths ranging from the surface to about 12 cm. Its siphons, though delicate, are extensible so that an animal 6–8 cm. deep can still project its siphon to the surface when this is covered with water. Animals lower than this have probably taken up a temporary position during low tide. *Mya arenaria* when young is found at depths similar to *Macoma*, but specimens 40 mm. or over are found some 30–50 cm. deep. Although they are then surrounded by mud almost devoid of oxygen and food, these can be obtained from a current of water drawn from the surface, through the ingoing channel of the extensible siphon. When the tide is in, *Mya* rises to within a few cm. of the surface and at low water it can be heard retreating deeper into the mud.

As at Parkgate, *Nereis diversicolor* is the dominant burrowing polychaete at Gayton and Heswall, but in addition there are *Pygospio elegans*, *Eteone longa* and *Ophelia* sp., and at Heswall the amphipod *Corophium volutator* is very abundant even in the waterlogged mud, where it cannot form permanent burrows.

(ii) Fauna of muddy sand (Table 5a)

The muddy sand appears to be a more favourable habitat since species and individuals are more numerous, except for *Hydrobia ulvae* and *Scrobicularia plana* which are rare. These species seem to have a mud preference which may be due to its higher silt content for feeding. *Corophium volutator* (with some *C. arenarium*) are as dense as 10,000 individuals per sq.m. of muddy sand in some regions.

The salinity of the interstitial water is similar to that of mud (29–30‰) but it is less subject to variation caused by fresh-water drainage from the land. The decrease in silt and subsequent coarsening of the texture probably accounts for the absence of turbellarians and ciliates, while at the same time it proves favourable to *Cardium edule*, and some polychaetes, though these are never very abundant per sq.m. and may be absent in large areas. Texture is not, of course, the only limiting factor, as tide level also plays an important part.

At Parkgate the muddy sand area is covered at each high tide, but in other regions—Heswall and Hilbre—part of this area remains exposed at neap tides for several days, so that the animals have to contend with dry conditions. The molluscs are active while the sand is moist (*Macoma balthica* may be seen burrowing through wet sand) but as it dries they retract into their shells and remain inactive. As observed previously, *Hydrobia ulvae* can survive dry conditions for over 2 weeks. This is also true of *Littorina littorea*, but

Table 5.

(a) Fauna of muddy sand

- NEMATODA 5–8 mm.
 OLIGOCHAETA
 Enchytraeids?
 POLYCHAETA
 Clitellio?
 Arenicola marina L.
 Pygospio elegans Claparède
 Ophelia sp.
 Eteone longa
 Nereis diversicolor Müller
 Nephtys caeca (Müller)
 MOLLUSCA
 Hydrobia ulvae (Pennant)
 Scrobicularia plana (da Costa)
 Macoma balthica (L.)
 Cardium edule L.
 Mya arenaria L.
 Abra alba (Wood)
 CRUSTACEA
 Carcinus maenas (Pennant)
 Corophium volutator (Pallas)
 Corophium arenarium Crawford
 DIPTERA
 Psychodid larvae (Parkgate)

(b) Fauna of clean sand

- NEMERTINI
 (*Prostoma*) *Tetrastemma* sp.
 NEMATODA 5–8 mm.
 POLYCHAETA
 Clitellio?
 Arenicola marina
 Pygospio elegans
 Ophelia sp.
 Nerine cirratulus (Della Chiaje)
 Scoloplos armiger (Müller)
 Eteone longa Fabricius
 Nephtys caeca
 Eulalia bilineata (Johnston)
 Phyllodoce macrophthalma Schmarda
 CRUSTACEA
 Crangon vulgaris L.
 Eurydice pulchra Leach
 Bathyporeia pelagica Bate
 Corophium volutator
 Haustorius arenarius (Slabber)
 MOLLUSCA
 Mya arenaria
 Macoma balthica
 Cardium edule
 Tellina tenuis da Costa
 Abra alba
 Hydrobia ulvae

laboratory experiments on *Macoma balthica* proved that larger individuals of this species only survive in a dry watch-glass at 65° F. for 4 days, while smaller (9 mm. or less) die after the second day. In the muddy sand, the temperature is lower and a certain percentage of water remains, so that *M. balthica* is able

to survive the dry periods by burrowing deeper (15–20 cm.) into the substrate. The lamellibranchs *Mya arenaria* and *Cardium edule* avoid desiccation by remaining below the surface of the muddy sand. The polychaetes and *Corophium* also burrow deeper into the sand during neap tides, so that at this time animals are rare in the top 5–10 cm. Generally *Corophium* is found from the surface to a depth of c. 18 cm., but under dry conditions none at all are found in this layer, the animals having burrowed into the damper muddy sand to a depth of 30 cm.

(iii) *Fauna of clean sand* (Table 5b)

At Parkgate the clean sand bordering low water is several hundred yards wide, but at Heswall and Hilbre it has become narrower and is mostly at a lower tide level. Parts of the marginal strip from Heswall to Hoylake are only covered by the equinoctial springs and there are raised bank regions in the strip bordering the main channel, which are at mid-tide level, so that tide level and salinity are important factors affecting the fauna. At Heswall, Caldy and West Kirby, sieving in the high sand regions revealed no fauna and the sand was very dry. Below about 15 cm. the substrate was coarse gravel unsuitable for burrowing forms. At Hoylake where the tide level of the clean sand at the base of the Red Rocks is lower and moist enough for a sparse population to exist, *Corophium volutator*, *Tetrastemma* sp., *Pygospio elegans* and *Eteone longa* were found.

Conditions in the sand bordering the main channel are more marine than elsewhere in the estuary. The sand is clean and unpolluted, and the salinity of the interstitial water is often as high as 30‰. The tidal water covering the area is between 25 and 30‰ even as far up the estuary as Parkgate. Hence truly marine species exist in these regions, while the muddy-sand species—*Nereis diversicolor*, *Hydrobia ulvae*, *Mya arenaria*, *Corophium* sp. and *Scrobicularia plana*—are rare or absent. This is due not to competition for space, since the animals are not as dense as in mud or muddy sand, but to the change in habitat, for example the increased salinity and lack of silt.

Distribution of marine forms in this region is controlled by tide level. Thus *Bathyporeia pelagica*, *Haustorius arenarius* and *Nerine cirratulus* are found only in high-lying (above mid-tide) dry sand, while *Tellina tenuis*, *Arenicola marina*, *Phyllodoce macrophthalma*, *Crangon vulgaris* and *Tetrastemma* are found only in the damp sand near L.W.M. (L.W.M. in the estuary is equivalent to 4 hr. flood tide). Other species in Table 5 are found in various numbers in all regions except the high dry sand where the fauna is often limited to *Haustorius arenarius* and *Bathyporeia pelagica*. The aquatic forms *Eurydice pulchra* and *Crangon vulgaris* are found in pools where these occur, but where the water drains away they burrow into the

damp sand and avoid desiccation. *Macoma balthica* is fairly abundant, but other molluscs are rare. *Arenicola marina* is the most abundant polychaete and may be as numerous as 12 per sq.m. in damper sand, though for the most part animals are very sparse in the clean sand.

As an animal community on the shore, the clean sand area of the Dee is comparable with the *Macoma balthica* communities of Petersen (1918) and Ford (1923), inasmuch as the four main species *M. balthica*, *Cardium edule*, *Mya arenaria* and *Arenicola marina* occur. The main difference in the Dee community is that *Cardium edule* and *Mya arenaria* are comparatively rare and are less dominant than crustaceans and polychaetes. Petersen also includes in his community, which occurs in sublittoral Danish waters, *Hydrobia ulvae* and *H. ventrosa* (Montagu). The latter species was not observed in the Dee, and *H. ulvae* is rare in the clean sand area and is not adapted to continual submersion in the Dee.

5. SEASONAL VARIATION AND QUANTITATIVE SURVEY: WITH BIOLOGICAL NOTES ON THE CHIEF SPECIES

Examination of seasonal variation was limited mainly to stations in three sectors, from Parkgate, Heswall and Hoylake Red Rocks respectively in a direct line to the main channel. Owing to the large area it was only possible to examine each station about every third week. Table 6 records the results of seasonal examination of the Heswall sector. The other tables may be referred to in my thesis (Stopford, 1949). The records are incomplete because the severe winter caused a covering of ice over the estuary for 3 months when sievings were impossible.

The occurrence and breeding seasons of several animals were recorded, but these cannot be taken as typical because of the unusually severe winter.

Cardium edule

Cockle beds in the estuary have not been as numerous in recent years. In counts taken in 1946 before December, about 1 per sq.m. *Cardium edule* occurred on the average in muddy sand and sand. During the winter the surface layer of water where it occurs was frozen and with the thaw in March large numbers of dead cockles were washed out of the sand. As a result only six adult specimens were found in all the post-winter sievings. The spat fall showed that the species was not entirely wiped out, though it may have come from other localities. On 26 June, a few specimens under 2 mm. across the shell appeared in sievings at Heswall so that spat fall began about a week before. Sievings were taken at the regular stations and also in clean sand areas which had become

covered with the temporary mud deposit and where the spat was therefore most likely to settle (Orton, 1937). By July, spat was also found at Parkgate and Hilbre (Hoylake). It was never numerous at Parkgate, but reached 1200 per sq.m. at Heswall in muddy sand and at Hilbre, first in the temporary mud deposits and later when this mixed to form muddy sand. This number is much below that recorded by Orton in 1937 (100,000 per sq.m.) perhaps because of the high adult winter mortality. The main spat fall occurred in mid-

July, though specimens less than 2 mm. were found until the second week in August, so that the fall extended over a period of 2 months beginning rather later than usual. Measurements of the largest specimens showed that these were 2 mm. long in late June; 3 mm. on 8 July; 5 mm. on 21 July, and 9 mm. by the second week in August, indicating a growth rate of about 4 mm. per month.

Orton (1933*b*) observed large numbers of dead or dying adult *Cardium* in the warm summer after the

Table 6. Results of seasonal quantitative estimation of fauna at the six stations on a transect from H.W. to L.W. off Heswall. Counts per $\frac{1}{4}$ sq.m.

	6 Nov. 46	9 June 47	24 June 47	11 July 47	30 July 47
Station 1					
<i>Pleurobrachia</i>				12 washed up	
Nematoda	20	20	50	.	200
Enchytraeidae?	.	6	.	.	30
Papillated <i>Clitellio</i> ?	.	1	250	340	100
<i>Ophelia</i>	.	.	.	4	.
<i>Arenicola marina</i>	1	.	.	.	.
<i>Pygospio elegans</i>	.	150	c. 150	40	36
<i>Nereis diversicolor</i>	9	1	3	20	32
<i>Nereis diversicolor</i> , 3 cm.	.	.	.	212	52
<i>Eteone longa</i>	.	5	50	32	.
<i>Corophium volutator</i>	1500	1500	5650	6000	1700
<i>Crangon vulgaris</i>	.	.	.	4	.
<i>Carcinus maenas</i>	.	.	.	4	.
<i>Hydrobia ulvae</i>	.	350	6	20 (dead)	460 (1400 spat)
<i>Mytilus edulis</i>	.	.	.	8 young	.
<i>Macoma balthica</i>	.	77	49	160	8
<i>Macoma balthica</i> (spat)	.	9	150	86	144
<i>Scrobicularia plana</i>	3	.	70 young	28 (16 spat)	8
<i>Abra alba</i>	8	.	.	.	.
<i>Mya arenaria</i>	6	6	25	.	28
Station 2					
<i>Ophelia</i>	.	.	.	1	.
<i>Arenicola marina</i>	.	2	1	4	2
<i>Pygospio elegans</i>	.	.	.	.	4
<i>Nereis diversicolor</i>	.	.	.	3 large, 3 small	.
<i>Eteone longa</i>	.	.	.	7	2
<i>Nephtys caeca</i>	.	.	.	.	2
<i>Corophium volutator</i>	.	.	1	3	1
<i>Bathyporeia pelagica</i>	.	3	3	.	3
<i>Crangon vulgaris</i>	.	.	.	1	.
<i>Hydrobia ulvae</i>	.	.	1	3	.
<i>Macoma balthica</i>	.	13	5	15	30
<i>Mya arenaria</i>	.	.	.	1	.
Station 3					
Nematoda	.	.	.	.	10000
<i>Tetrastemma</i> sp.	.	.	.	.	1
<i>Arenicola marina</i>	.	2	3	.	.
<i>Pygospio elegans</i>	.	12	21	.	.
<i>Nereis diversicolor</i>	.	3	2 large, 5 small	.	16
<i>Eteone longa</i>	.	30	82	.	.
<i>Nephtys caeca</i>	.	.	1	.	.
<i>Corophium volutator</i>	.	50	600	.	650
<i>Hydrobia ulvae</i>	.	43	10	.	156
<i>Macoma balthica</i>	.	43	56	.	8
<i>Macoma balthica</i> (spat)	.	.	184	.	12
<i>Cardium edule</i> (spat)	.	.	11	.	12

Table 6 (cont.)

	6 Nov. 46	9 June 47	24 June 47	11 July 47	30 July 47
Station 4					
Nematoda	.	.	.	80	200
Enchytraeidae	.	.	.	400	.
<i>Clitellio?</i>	.	.	12	24	48
<i>Pygospio elegans</i>	.	.	376	332	436
<i>Nereis diversicolor</i>	.	.	4	24 large 80 small	36 large 16 small
<i>Eteone longa</i>	.	.	208	16	40
<i>Corophium volutator</i>	.	.	4200	3200	2400
<i>Carcinus maenas</i>	.	.	.	.	4
<i>Hydrobia ulvae</i>	.	.	736	72	600
<i>Mytilus edulis</i>	.	.	.	.	4
<i>Macoma balthica</i>	.	.	64	12	56
<i>Macoma balthica</i> (spat)	.	.	212	80	188
<i>Mya arenaria</i>	.	.	4	.	124 (small)
<i>Abra alba</i>	.	.	8	.	.
<i>Cardium edule</i> (spat)	.	.	20	.	448
<i>Tellina tenuis</i>	.	.	4	.	.
Station 4A					
Nematoda	.	.	.	60	.
<i>Clitellio?</i>	.	.	.	100	.
<i>Pygospio elegans</i>	.	.	.	600	.
<i>Nereis diversicolor</i>	.	.	.	4	.
<i>Eteone longa</i>	.	.	.	40	.
<i>Corophium volutator</i>	.	.	.	1600	.
<i>Hydrobia ulvae</i>	.	.	.	20	.
<i>Macoma balthica</i>	.	.	.	60	.
<i>Macoma balthica</i> (spat)	.	.	.	184	.
<i>Cardium edule</i> (spat)	.	.	.	32	.
Station 5					
Nematoda	.	.	.	.	20
<i>Tetrastemma</i>	.	.	.	2	.
<i>Arenicola marina</i>	.	1	.	.	3
<i>Pygospio elegans</i>	.	.	.	4	100
<i>Eteone longa</i>	.	.	.	.	55
<i>Corophium volutator</i>	.	3	.	2	64
<i>Bathyporeia pelagica</i>	.	3	.	88	34
<i>Haustorius arenarius</i>	.	.	.	2	.
<i>Eurydice pulchra</i>	.	.	.	151	.
<i>Carcinus maenas</i>	.	.	.	.	2
<i>Hydrobia ulvae</i>	.	.	.	.	10
<i>Hydrobia ulvae</i> (spat)	.	.	.	.	1002
<i>Mytilus edulis</i>	.	.	.	.	1
<i>Macoma balthica</i>	.	8	.	.	36
<i>Macoma balthica</i> (spat)	.	18	.	.	18
<i>Cardium edule</i> (spat)	.	.	.	2	47
Station 6					
<i>Clitellio?</i>	.	.	.	.	5
<i>Arenicola marina</i>	.	.	.	1	.
<i>Arenicola marina</i> (young)	.	.	.	3	.
<i>Pygospio elegans</i>	.	.	.	10	7
<i>Eteone longa</i>	.	.	.	4	4
<i>Nephtys caeca</i>	.	.	.	4	3
<i>Phyllodoce macrophthalma</i>	.	.	.	.	1
<i>Corophium volutator</i>	.	.	.	3	50
<i>Bathyporeia pelagica</i>	.	.	.	5	.
<i>Eurydice pulchra</i>	.	.	.	.	1
<i>Hydrobia ulvae</i>	.	.	.	.	3
<i>Hydrobia ulvae</i> (spat)	.	.	.	.	7
<i>Macoma balthica</i>	.	.	.	13	12
<i>Macoma balthica</i> (spat)	.	.	.	.	1
<i>Cardium edule</i> (spat)	.	.	.	.	3

breeding season. Owing to the mortality of the adults in the previous winter, no similar observations could be made in the summer of 1947.

Scrobicularia plana

This bivalve also lives in the surface layer and like *Cardium edule* suffered in the severe winter. In 1946 the species occurred in the mud and muddier sand at Heswall and Hilbre at a density of 1 per 4 sq.m., but after the winter it was very rare. Spat under 2 mm. long was indistinguishable from that of *Macoma balthica*, but a few larger specimens (2–4 mm.) of *Scrobicularia plana* spat were recorded in Heswall mud during June and July.

Macoma balthica

This mollusc is a more active burrower than the two previous species and by burrowing deeper into the substrate was better able to survive the winter, so that it was abundant throughout the year. Although it is found in substantial numbers in all areas, it has a preference for mud, and thus in Heswall mud 640 adults were found per sq.m., whereas on the same date there were only 90 per sq.m. in the clean sand, and the largest specimens (20–23 mm.) were more numerous in mud. Its absence from the Parkgate mud is probably due to the higher tide level and sewage content.

Spat fall occurred earlier than that of *Cardium*, in the second week of May. The fall was heaviest in June and July when over 2000 were found per sq.m. of mud. Spat was more common in mud and very rare in clean sand. By August the smallest spat were 4 mm. long and so it was assumed that settling had ceased. Growth is more rapid in the summer so that by December early spat is about 10 mm. long, while late spat is about 4 mm. Maturing gonads were found in all specimens during the winter and spring except in those under 12 mm. long, which were taken to be under 1 year old.

Macoma balthica, which lives in all types of areas, at almost all tide levels and with a 3-month heavy spat fall, is the dominant animal species in the estuary.

Mya arenaria

This bivalve lives deeper in the mud than any of the species mentioned above and hence survived the winter. Small individuals about 6 mm. long were found at the beginning of June and may have been 1947 spat, but no smaller specimens were found before this date. The first definite spat fall was recorded at the end of July, when 50 specimens under 2 mm. long together with 76 specimens between 3 and 6 mm. long were found per sq.m. of mud. The young forms were all found within the top 10 mm. layer of mud. Hence

the distribution of the species in depth is correlated with the size of the individual (cf. length of siphons).

Hydrobia ulvae

This snail is also a dominant species, having a similar distribution to *Macoma balthica*. It is possible that more than one species of *Hydrobia* occurs, since some individuals were larger and possessed a more pointed spiral, but this may merely be a variation and all specimens were recorded as *H. ulvae*. This is the only species recorded in the estuary (McMillan, 1941*a*) where the salinity is considerable. McMillan (1941*b*) records *Hydrobia jenkinsi* at Burton marshes where the gutters are only slightly salty. Boycott (1936) states that fresh-water strains of *H. jenkinsi* may easily be got to live and breed in salt water, but the individuals found in the estuary did not fit the description of this species.

The adult *Hydrobia* suffered a great mortality in November, when hundreds of empty shells were observed. This was not due to the severe winter, which did not begin until January. Live specimens were rare in sievings from November until the following spring, when they became numerous. It is possible that the spring population is formed from small individuals which survived the winter burrowed in the substrate and escaped through the sieve because of their small size.

The first egg-carrying individuals were observed on 12 May 1947. Individuals collected on 18 April and kept alive in the laboratory laid eggs by 10 May, so that the onset of spawning was the first week in May. The eggs are carried in clumps on the shell and are protected by a covering of fine sand. Similar eggs were found on small pebbles at Heswall and on empty shells, but unfortunately these did not hatch, so that their identity was not established. If they were *Hydrobia* eggs, it would suggest that the animal does not lay its eggs on its own shell, but on that of a neighbour, or a substrate of similar nature. On the other hand, the larger specimens (4–5 mm.) carried eggs first, which indicates that animals lay eggs on their own shells, since one would expect larger animals to mature first.

Specimens bearing eggs were found from May to the first week in August, but the majority (83 %) were egg-bearing in June and early July. Towards the end of July, the percentage decreased, and on 9 August less than 10 % were egg-bearing.

In the laboratory eggs took between 8 and 10 days to hatch, but the veligers died after about a week. Spat fall is difficult to detect since early spat is almost microscopic and passes through a 0.5 mm. sieve. Even specimens 0.5 mm. long may escape, as their width is much less. A few young specimens were first found in July, about a month after the first eggs were seen, but at the end of July, spat under 1 mm. long were as

dense as 7440 per sq.m. of muddy sand. This indicates that there is a period of just over 1 month between the appearance of the eggs on the shell and the spat fall.

Unlike *Cardium* and *Macoma* spat, *Hydrobia* is found on all types of substrate. It is more numerous in mud and muddy sand, but even in clean sand areas there were 30–40 spat per sq.m.

Corophium volutator

Although this amphipod is not as widespread as *Macoma* and *Hydrobia*, *Corophium volutator* is probably the most numerous species in the estuary. It is rare or absent in clean sand, but exists in thousands (24,800) per sq.m. across the wide expanse of mud and muddy sand below H.W.N. Elmhirst (1932) found that this species was limited to H.W. at Millport, but in the Dee it extends well below this line and it is probable that silt content is an important factor in its distribution. *C. arenarium* is the only other species of *Corophium* found in the estuary. It is limited to the clean sand by Hoylake Red Rocks and to regions of muddy sand towards Hilbre at a similar tide level—just above H.W.N.—and is never found in large numbers.

Moore & Spooner (1940) and Beanland (1939) record *C. volutator* in the Tamar and Dovey estuaries respectively, but only in small numbers, stating that they are only found in sheltered areas. Lack of shelter does not appear to be a limiting factor in the Dee, since *Corophium* is abundant along the unsheltered foreshore.

C. crassicornis and *C. grossipes* L. (together with Sponges, Hydroids and Anemones) which are absent in the Dee are recorded in the Tamar (Percival, 1929), where the water is less polluted and where typical marine forms are found well up the estuary because of the comparatively high salinity (21–35 ‰).

In the Dee, females of *C. volutator* were always more numerous than males and they reached a greater size. In July there were 5800 females to 200 males (3.3% males) per 0.25 sq.m. Mature females were observed carrying eggs from 19 May to 11 August, when shore collecting ceased. The number of eggs carried on the abdomen varied directly with its size, the average (about 6 mm. long from tip of head to telson) carried about 20 eggs. The percentage of egg-bearing females was low (5%) at first, but rose to 70% in mid-June. It had dropped to 40% by the end of July and was only 10% by the first week in August. The young were too small to be retained in the sieve, but small individuals were observed escaping from the sieve on 24 June. These were about 1–2 mm. long and were probably hatched from the first May eggs.

During June and July numerous dead, mainly male, *Corophium* (not exuviae) were found in shallow pools and channels. This high mortality after the breeding season, together with the fact that males are

comparatively few and have a small maximum size, suggests that they are annual forms which do not survive the winter. There seems to be some doubt as to whether adult males or females survive the winter. Watkin (1941) states that mature forms die off after breeding and the new generation breeds the following March. Hart (1930) observes a tendency for mature forms to die in autumn and winter—particularly the males. This seems borne out by observations on the Dee, although large populations (500 per 0.25 sq.m.) were found throughout the winter. These, however, may have been the early generation of the previous spring.

Bathyporeia pelagica

This amphipod is found only in clean sand above and below H.W.N. It is similarly confined to the upper half of the intertidal zone in loose sand at Millport (Elmhirst, 1931); salinity, tide level and absence of silt being factors controlling the occurrence of this species. There, as in the Dee, it is generally associated with *Haustorius arenarius*. Watkin (1938) describes *Bathyporeia pelagica* and also observes that it is restricted to sandy regions below H.W.N. in Redcar, Scotland and the west coast of Wales. Hence it is more a coastal than an estuarine form. *B. pelagica* has a similar breeding period to *Corophium volutator*. Females bearing 6–12 eggs were found from 27 May until 15 August when shore collecting ceased, and they were most numerous in June and July. The eggs are blue and are conspicuous both in the ovary and when carried under the abdomen. It was difficult to assess the true proportion of each sex, since only about 12 specimens were found per 0.25 sq.m., but it appeared that males were slightly fewer than females.

Polychaeta

Breeding was not studied in the polychaetes, but their distribution throughout the estuary was observed.

Arenicola marina occurs mainly in clean sand below mid-tide and especially in damp muddier sand at the same tidal level. Hence it is tide level more than type of substrate which controls its distribution, and its absence from regions near fresh-water drainage channels shows that salinity is also a controlling factor. Experiments by Reid (1929) showed that *A. marina* became turgid in water of 14.32 ‰ salinity so that it was unable to burrow.

Nereis diversicolor has a wide distribution, occurring in all types of substrate. It is very numerous in the mud and muddy sand regions down to mid-tide, but it is rare in clean sand by the main channel where there is less exposure. It is evidently the high salinity of the latter region which acts as an adverse factor, since it survives well in almost continuous submersion in dilute sea water near the fresh-water drainage channels. Moore & Spooner (1940) also observe that

it is most common between mid-tide and H.W.N., but that it can survive continuous submersion in brackish water. Its preference for a lowered salinity limits *N. diversicolor* to an estuarine habitat and it is comparatively rare in coastal regions (Pirrie, Bruce & Moore, 1932).

Thorson (1946) observes that *N. diversicolor* breeds all the year round in Cherbourg, but evidence from Table 6 indicates a spring–summer breeding season in the Dee, as more small and therefore presumably young individuals occur in June and July.

Pygospio elegans and *Eteone longa* are the most abundant polychaetes in the estuary; both are small and may occur in large numbers (over 2000 per sq.m.). They are adapted to similar conditions and though having different habits (the former being Sedentaria and the latter Errantia) they occur in the same sort of ground. They are the only polychaetes ranging over all tide levels and all types of substrate and are absent only in Parkgate mud, where pollution is high. They are most numerous in mud and muddy sand. The numbers decrease towards clean sand, very few being present in the higher-lying regions of the latter. Bassindale (1938) and Corlett (1948) record *P. elegans* in soft mud in the river Mersey. In most estuaries *Polydora ciliata* (Johnston) has a similar distribution to *Pygospio elegans*. No specimens were identified as *P. ciliata* in the Dee; but owing to the large numbers, all specimens were not closely examined and it is not impossible that *P. ciliata* occurs in the Dee estuary, particularly as it has been recorded in the Mersey (Corlett, 1948).

Rees (1940) records an entirely different set of polychaetes in the Bristol Channel, while Salcombe flats are limited to fewer species, *Myrianida*, *Noto-mastus* and *Melinia* being the dominant genera (Allen & Todd, 1900).

Other polychaetes in the Dee are comparatively rare or limited in their distribution. *Ophelia* sp. occurred in mud and muddy sand at Heswall and Hilbre in numbers of about 20 per sq.m.

Scoloplos armiger, *Nephtys caecae* and *Nerine cirratulus* are only found in clean coarser sand near low tide mark towards the mouth of the river and each species rarely exceeds a density of 12 individuals per sq.m.

Oligochaeta

Several oligochaetes are found in mud and muddy sand. These were not identified, though four species were recognized. Small (2 mm.) white, and larger (4–6 mm.) pink, Enchytraeid-like forms were found mainly in muddy regions, while larger reddish Oligochaeta, smooth or papillated, were found both in mud and muddy sand and were often numerous. Fraser (1932) observed *Clitellio arenarius* Müller in abundance in similar regions in the Mersey, so that possibly the larger worms in the Dee were this species.

6. COMPARISON BETWEEN THE MERSEY AND DEE SHORE FAUNA

The Mersey estuary, lying roughly parallel to the Dee, has to some extent similar conditions and fauna. The same tide supplies both estuaries, which lie on either side of the Wirral peninsula, though the currents differ owing to the bottle-neck of the Mersey, which divides it into an outer and an upper estuary (defined by Bassindale, 1938).

The outer estuary, lying north-west from Wallasey and Gladstone Dock, has more marine conditions than any part of the Dee estuary. The intertidal zones are sandy and the salinity is about 32.4 ‰,—greater than at the mouth of the Dee where it is about 30 ‰. Hence marine forms such as Hydrozoa, sea-anemones, the polychaetes *Owenia* and *Pectinaria*, the echinoderms *Echinocardium* and *Ophiura* and several molluscs—*Montacuta*, *Donax*, *Macra* and *Chione* occurring in the outer estuary of the Mersey are rare or absent from the Dee. Conditions at the mouth of the latter, around Hilbre Island, are the most comparable with those of the outer Mersey estuary and such forms as *Nereis diversicolor*, *Nephtys* spp., *Scoloplos armiger*, *Pygospio elegans*, *Eurydice pulchra*, *Macoma balthica*, *Cardium edule* and *Mya arenaria* occur in similar numbers in both regions. A few species (*Bathyporeia pelagica*, *Haustorius arenarius*, *Tellina tenuis* and *Abra alba*) found at the mouth of the Dee are not recorded in the Mersey.

Polydora ciliata, found settling in large numbers on the jetty in the Mersey by Corlett (1948), was not observed in the Dee, nor is it recorded by the other collectors on the Mersey foreshore (Fraser, 1932; Bassindale, 1938).

The upper estuary of the Mersey, where it widens above Dingle Point, is similar to the Dee estuary at Parkgate and Heswall. The salinity is less than 20 ‰ and both estuaries measure several miles across and have a large intertidal zone in this region. In the Mersey, however, sewage and silt content are far greater than in the Dee, and the shore of the former is mainly mud and stones. The Dee shore is generally sandy, mud is limited to an area bordering the banks and stones are rare. The high content of silt in the Mersey (Fraser, 1938) reduces the light penetration, hence the only alga recorded is *Fucus vesiculosus* (Bassindale, 1938); while in the Dee lack of stones for algal settlement limits its occurrence to the rocks at Heswall, Caldy and on Hilbre Island. The most characteristic flora of the Dee is the marshland from Burton to Gayton, which has an important influence on the distribution of fauna and the state of the substrate. Marsh plants do not form an important feature of the Mersey (Bassindale, 1938), although the marsh at Frodsham which serves for cattle grazing may be similar to that at Burton, since it is flooded at H.W.S.

The fauna of the mud and muddy sand in the upper regions of the two estuaries is very similar, although the stones in the Mersey give foothold to *Mytilus edulis*, *Littorina littorea* and barnacles which are rare in the Dee. *Hydrobia ulvae* occurs in vast numbers in both estuaries, though whereas in the Dee it is rare in the more marine conditions towards the mouth, it extends in large numbers into the outer estuary of the Mersey round to Hightown and Hoylake (Bassindale, 1938). *Corophium volutator* is also very numerous in both estuaries, while *C. arenarium* is found only in the Dee. Mersey molluscs are dwarfed, and Fraser (1932) suggests that this is due to competition for space. Counts of fauna per sq.m. in the Dee, where there is no dwarfing, are higher, but the habitable depth is about 15 cm.—more than twice that in the Mersey.

The faunas of the Dee and the Mersey are therefore similar, although salinity, variation in currents and silt content act as limiting factors for some species.

7. ACKNOWLEDGEMENTS

The practical work was carried out in the Department of Zoology, University of Liverpool, under the guidance of Prof. J. H. Orton, to whom I am indebted for invaluable suggestions and criticism. My thanks are also due to Prof. E. A. Spaul for helpful interest, to Captain G. Wright (Chester) for the loan of copies of the early River Dee maps, and to Dr N. S. Jones for confirming amphipod identifications.

8. SUMMARY

1. The Dee estuary is wide and funnel-shaped, with a large intertidal area. Historical records show that it has been continually changing, to a large extent as a result of control by man. Silt is being deposited along its banks and marshland is encroaching on the foreshore.

2. The factors controlling the presence and distribution of fauna are: salinity, tide level and exposure, silt content and texture, pollution.

3. The salinity varies about 5‰ in the main channel throughout the year. It is about 30‰ towards the mouth of the river where a true marine fauna occurs and gradually decreases upstream to about 20‰ at Burton Point and then, in the New Cut, drops suddenly to less than 1‰ at Queensferry. The salinity of small volumes of free water in pools and channels at low tide varies greatly, but that of the intertidal water of the substrate remains fairly constant.

4. The entire estuary is at a high tidal level and the foreshore is exposed for about 10 hr. a day, when the only protection is offered by the marsh flora. This accounts for the general absence of permanent surface

dwellers. Insects and spiders are found in marsh areas, but elsewhere the surface dwellers are limited to *Hydrobia ulvae* and *Carcinus maenas*. Rocks supporting Hydrozoa, Polyzoa and barnacles are found only in a small area at Heswall and Hilbre Point.

5. The substrate is divisible into three main types—mud, muddy sand and clean sand—according to the silt content. The mud runs along the banks and is generally about high tide level; the muddy sand covers the largest area and lies between mid-tide and H.W.N.; and the clean sand is mainly confined below this level, nearer mid-estuary. Variations in the tidal currents cause shifting of banks and temporary deposits of silt in sandy areas.

6. Pollution is not excessively high and is probably a less important factor than it is in the more industrialized river Mersey, although the amount of chemical effluents passing into the Dee is not known. Sewage may have a strong local effect.

7. The fauna of the shallow pools and channels is limited because of the great variation in temperature and salinity. In the pools, which are liable to drain or evaporate during low tide, the animals, apart from ciliates and small copepods, are either equipped to withstand a certain amount of exposure—*Obelia gelatinosum*, Mollusca, *Carcinus maenas*, barnacles, insects—or they are capable of burrowing into the underlying wet sand to avoid desiccation—*Crangon vulgaris*, nematodes, polychaetes, amphipods. The variation of salinity in the channels is mainly due to fresh-water drainage from the banks and it limits the species to such forms as *Carcinus maenas*, *Gammarus duebeni*, *Crangon vulgaris* and *Gobius minutus*.

8. The substrate forms a more stable medium and hence the majority of species in the estuary are burrowing forms. Their distribution is controlled by tide level and the silt content of the substrate. Lack of oxygen in the lower layer of mud may be a controlling factor for many species. Generally speaking the mud along the banks is at a higher tidal level, giving way to muddy sand and finally clean sand towards low water. A few species occur in all types of substrate, namely *Nereis diversicolor*, *Macoma balthica* and *Hydrobia ulvae*, but they are more numerous in mud and in general mud species are absent from the clean sand. The presence of silt proves favourable to the detritus-feeding forms *Corophium volutator* and *Hydrobia ulvae* which occur in large numbers in muddy areas. The spat of many molluscs occur most often in silt even when the adults, e.g. *Cardium edule*, inhabit clean sand. This is possibly because they are deposited with the silt where the current is slack.

9. Observation on hatching and spat fall of *Hydrobia ulvae*, *Macoma balthica* and *Cardium edule* indicate that these start in early June and finish at the end of July or early in August, but this may be

later than usual, owing to the severe winter which persisted until mid-April 1947.

10. The most abundant species found in the estuary are: *Hydrobia ulvae*, *Macoma balthica*, *Cardium edule*, *Corophium volutator*, *Nereis diversicolor*, *Arenicola marina*. There is a notable absence of

sponges and sedentary coelenterates, and since these occur in the Mersey the cause is probably the absence of rock substrate.

11. A seasonal study of animals at regular stations was carried out throughout the year.

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THE DISPERSAL OF *URCEOLARIA MITRA* (PERITRICHA) EPIZOIC ON FLATWORMS

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(With 1 Figure in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	123	5. AN ANALYSIS OF DISPERSAL METHODS	126
2. THE URCEOLARIAN POPULATION OF NEWLY HATCHED FLATWORMS	124	6. THE NATURAL INFESTATION OF FLATWORMS AND THE BUILDING UP OF THE URCEOLARIAN POPULATION	128
3. DISPERSAL UNDER LABORATORY CONDITIONS	124	7. DISCUSSION	129
4. <i>URCEOLARIA MITRA</i> AS A FREE-LIVING ORGANISM.	124	8. ACKNOWLEDGEMENTS	130
(a) In the plankton	125	9. SUMMARY	130
(b) On the substratum	126	REFERENCES	130
(c) Duration	126		

1. INTRODUCTION

Urceolaria mitra Von Sieb belongs to the peritrich family of Protozoa, the Urceolaridae, and according to Hirshfield (1949) eleven species have been recorded, all from invertebrates. Nine occur on marine hosts, one on a land-snail, while *U. mitra* is the only freshwater species. Some of the Urceolarids, particularly those belonging to the genus *Trichodina*, are definitive parasites of fish, while others such as *Urceolaria mitra* are better referred to as epizoic for the time being. The latter is found on the surface of flatworms and occurs most abundantly on the triclad *Polycelis tenuis* Ijima (Reynoldson, 1947, 1948). These peritrichs move freely about the dorsal surface and when stimulated, for example by light, become very active. A series of typical shapes is shown in Reynoldson, (1950, Fig. 1). A preliminary account of its seasonal population fluctuations has been given already (Reynoldson, 1950) together with the references to the biology of these organisms. The small, ornamental pond in the grounds of the Memorial Buildings, Bangor, where the observations on dispersal were made, was also described in that paper.

The early population work on *Urceolaria mitra*, done outside the breeding season of the flatworm and when the peritrich population was high, showed every specimen of *Polycelis tenuis* to be infested. But this incidence was reduced later because young worms were often without the epizoite. It also declined during periods of population depression of the peritrich when worms of all sizes were found free. These points receive attention in the paper already referred to, but the problem of dispersal vital to an understanding of population fluctuations is examined in

more detail here. 'Dispersal' is used in this account in the sense of spread *within* a single community of flatworms and not from one separate community (e.g. pond) to another.

The simple life cycle of the Urceolaridae, without any known resting or internal stages (Richardson, 1938; Hirshfield, 1949) and multiplication by binary fission, suggests that dispersal might occur by free-swimming individuals. Apart from a detailed paper on the spread of *Urceolaria patellae* (Brouardel, 1947) to be discussed later, there are few data on the method and time of the infestation of new hosts by Urceolarians. Previous work suggests that members of the genus *Trichodina* are much more prone to leave their hosts and become planktonic. Thus Clark (1866) reported that *T. pediculus* frequently leaves *Hydra* to become free-swimming. Keiser (1921) also found *Trichodina steinii* apart from its flatworm host, while Wang (1928) collected *Trichodina* sp. with pond plankton. In contrast, Keiser never found *Urceolaria mitra* apart from its host and reported that its shape was less suitable for free movement than that of *Trichodina steinii*. This viewpoint seemed to be fully borne out by the behaviour of *Urceolaria mitra* in current experiments when it was only once seen to leave its host voluntarily.

It is clear that, Brouardel's work excepted, there is very little information about how urceolarians reach new hosts and no experimental evidence. Therefore in this account an attempt is made to examine all possible methods. The condition of newly emerged flatworms has been studied in the laboratory and in the field, while the building up of the epizoic population in time has been followed. This showed that there was no complication in the life cycle and so possible

dispersal by individuals (a) being free-swimming, (b) living on the substratum, (c) spreading by host contact, has been examined.

The examination of water for free-living *Urceolaria* is difficult owing to their habit of attaching themselves to the substratum—consequently in many experiments flatworms cleaned of the epizoite were used as 'traps' to pick up *U. mitra*. For this purpose a few minutes immersion in 0.02% chromic acid was effective, causing the *Urceolaria* to drop off while leaving the flatworm unharmed. In all experiments when testing for the presence of *U. mitra* half the worms prepared as 'traps' in this way were used as controls to check that all the *Urceolaria* originally present had been removed. In no case did the chromic acid fail to remove all the epizoites.

As a result of observations by Dr Y. Melander (private communication) a re-examination of *Polycelis tenuis* suggests that the pond population used in the experiments included a minority of a hybrid between *P. tenuis* and *P. nigra*. However, not only are the urceolarian populations of the two forms numerically similar but they both attract free-swimming *Urceolaria* to an equal degree. For the purposes of this paper the two flatworms can be considered together.

2. THE URCEOLARIAN POPULATION OF NEWLY HATCHED FLATWORMS

The possibility of *Urceolaria mitra* occurring within the cocoons of *Polycelis tenuis* and infesting young worms before hatching appeared remote, in view of the simple life cycle of the protozoan and of the demonstration that young worms were frequently not infested (Reynoldson, 1950). But to test this, mature worms collected from the pond were divided into two batches, one of which was treated with chromic acid to remove the *Urceolaria*. Each worm from the two batches was kept in a Petri dish and the cocoons collected. Within 24 hr. of hatching the emerged worms were examined for *U. mitra* in a well slide, using chromic acid; the relatively large size of the peritrich permitted easy counting under a low-power binocular microscope. Ten cocoons from which thirty-eight worms emerged were produced by the batch treated with chromic acid, twelve cocoons with fifty-six young by the untreated worms. None of the young worms was infested and it would appear that emerging worms were free from the epizoite. To make quite certain that this was not produced by unfavourable laboratory conditions, cocoons deposited in the field were collected and kept until hatching. None of the thirty-three worms emerging from twelve cocoons was infested. Finally, observations were made on cocoons deposited in the field and permitted to hatch in cages in the pond. Eighteen cocoons were used and thirty-nine young worms examined.

The low number of worms relative to cocoons resulted from the escape of some through the mesh of the bolting silk cage. With one exception all the newly emerged worms were negative—one individual carried a single *U. mitra*. The significance of this is considered later, but it does not invalidate the conclusion that newly hatched flatworms are free from *Urceolaria* and have to become infested from outside sources.

3. DISPERSAL UNDER LABORATORY CONDITIONS

A simple experiment was made to see if *U. mitra* would spread from one flatworm to another, and if so the rate at which it occurred. Five adult infested flatworms were kept with another five adult worms cleaned of *Urceolaria* by chromic acid treatment, in a Petri dish 12 cm. in diameter. All the infested worms chosen were dark in colour, the treated individuals light-coloured so that they could be distinguished after mixing. It has been shown that under natural conditions the urceolarian population is similar for light- and dark-coloured worms.

In the first experiment the Petri dishes were set up in triplicate and examined at 2, 4 and 8-day intervals. In a second experiment they were examined at 1, 3 and 6 days. These experiments were repeated except that young treated worms were used instead of adults. Under such simple conditions the rate of spread of *U. mitra* from infested to non-infested worms was fairly rapid. By the fourth day the numbers on both groups were equal and thereafter no distinction was maintained. The spread to young worms was much slower and after 7 days distribution was still unequal. From such an experiment it cannot be determined whether dispersal occurred by free-swimming individuals or by spreading while worms were in contact. The flatworms showed aggregational behaviour in the dishes just as they do in nature. The reason for the slower spread to young worms is not clear, but may result from their smaller size providing less 'contact' area, and from differences in activity due to age.

A variable number of *Urceolaria* on the individual infested worms is a common feature of this epizoid population. It has been found that while the general level of the population fluctuates, at any one time that of individual worms has a wide range.

4. URCEOLARIA MITRA AS A FREE-LIVING ORGANISM

When *U. mitra* is brushed from its host it often becomes attached to the bottom of the vessel, but some individuals swim actively. Zick (1928) has described the movement of *Urceolaria* species and,

as Kepner & Pickens (1925) have also noted, it swims with the aboral surface in front, moving in an anti-clockwise direction around the anterior-posterior plane at the same time. The last point was not mentioned by Kepner & Pickens, who also erroneously named the species *Trichodina steinii*. Fauré-Fremiet (1943) noted, from their figures, that it was a species of *Urceolaria*, probably *U. mitra*. Thus, while contact between the flatworms seemed to afford the likeliest opportunity for dispersal, it was also necessary to determine if *U. mitra* occurred in the plankton.

(a) *In the plankton*

The first attempt to test this was by keeping non-infested worms in cages in the pond. This method failed because it was difficult to isolate the worms from all contact with the natural population while leaving the *Urceolaria* reasonable access. However, the results show the rapidity with which re-infestation can occur under conditions more stringent than in nature. Simple cages of glass tubing 3×2.5 cm. closed at each end by bolting silk and suspended on fine fuse wire from a wire tripod were first used. These contained two cleaned flatworms. Out of twenty-six cages each exposed for 1 week, twenty-six of the fifty-two worms had become infested. The average number of *Urceolaria* per worm was 3.0. Such dispersal could have occurred either as the result of contact with the natural worm population or by free-swimming *Urceolaria*. In a more stringent test using one such cage inside a larger one, worms still became infested. Out of fifteen tests using thirty worms, after a week's exposure ten became re-infested with an average of 2.5 *Urceolaria* per worm. The slower dispersal probably reflected the greater isolation of the worms, but again it was impossible to exclude small worms from the inner cage and spread by contact may have occurred.

The only certain method of determining if *Urceolaria* becomes planktonic is to recover it from pond water. All efforts to find *U. mitra* in pond water by direct examination following concentration failed. A different technique was used therefore, in which five cleaned flatworms to attract the *Urceolaria*, were added to 500 c.c. of pond water, previously strained to exclude extraneous flatworms. The experiment was made in wide-mouthed jars. The worms were examined for *Urceolaria* after 5 days, on the assumption that any occurring in the water would attach themselves. Each of twenty such tests proved negative, and it appeared that if *U. mitra* occurred free-swimming then there were small numbers only. To examine larger volumes of water concentration was employed by filtering through paper in a sinter-glass funnel, using suction. The filter-paper, which would carry any *Urceolaria*, was transferred to a Petri dish and filtered pond water together with five

cleaned worms added. As before, the worms were examined after a 5-day interval, with the following results:

Volume of water filtered (l.)	No. of tests	No. of positive results	No. of <i>Urceolaria</i>
1	17	6/85	2, 2, 1, 3, 4, 1
2	15	2/75	2, 4

Thus it must be concluded that *U. mitra* does occur in the plankton in small numbers. The efficacy of this method in determining the presence of *Urceolaria* was examined by adding known numbers of *U. mitra* to filtered pond water and then carrying out the procedure outlined above. Out of ten tests, five positive results were obtained and if it is assumed that the peritrich did not multiply after becoming attached (§5), 30% of all added *Urceolaria* were recovered. Application of this recovery figure to the results above gives an average of one *U. mitra* per litre of pond water. Although it must be regarded as very approximate, this figure seems reasonable in the light of available evidence.

A second line of inquiry examined the ability of *U. mitra* to disperse by free swimming in the laboratory. The apparatus consisted of two glass cylinders 5.5 by 5.5 cm., the ends closed by bolting silk. These two cages were held together by rubber bands and the two adjacent ends were separated by a Perspex ring 0.75 mm. thick, to prevent contact between the flatworms in each cage. One of these contained fifteen infested flatworms, the other fifteen cleaned worms. Only large individuals were used, to prevent escape from the cages through the bolting silk. The two conjoined cages were immersed in strained pond water in an aquarium. After 4 days the number of *Urceolaria* on the flatworms in each cage was counted. In a second series of experiments a wider Perspex ring 3 mm. thick was used, giving a greater distance for the *Urceolaria* to cross (Table 1). Such an arrangement would not at first sight prevent *Urceolaria* from gliding over the surface of the Perspex rings and so reaching the uninfested worms; but when separated from its host the peritrich seems incapable of such movement; it either swims actively or remains attached to the substratum.

There was considerable variation in the total *Urceolaria* on the infested worms, which reflected partly the level of the epizoid population in the pond at the time of the experiment and partly the success in keeping them alive during the experiment. The results show conclusively that *U. mitra* does leave its host and swim, passing distances of 0.75 and 3 mm. across the two inner barriers of bolting silk.

Thus both field and laboratory data support the conclusion that *U. mitra* will leave its host and become

a member of the plankton in small numbers for some period. Dispersal may result from this habit, and the newly hatched *Polycelis* found with one *Urceolaria* (§2) may have acquired it in such a way.

Table 1. *Dispersal in water*

Exp.	Total no. of <i>U. mitra</i> on infested worms	Total no. of <i>U. mitra</i> on cleaned worms	No. of cleaned worms becoming infested
1a	221	0	0
2a	158	1	1
3a	30	1	1
4a	14	2	2
5a	10	0	0
6a	9	0	0
7a	215	8	7
8a	268	21	11
1b	231	28	11
2b	221	24	13

Thin Perspex rings were used in series *a*, thick rings in series *b*.

(b) *On the substratum*

The demonstration of *U. mitra* as a member of the plankton free from its host suggests that it might also live for some brief period on the substratum or vegetation of the pond, and re-infest flatworms as opportunity offered. This point was examined by taking five samples of substratum from different parts of the pond. Each sample, amounting to 10 c.c. of liquid mud and debris, was first carefully examined for flatworms partly by baiting with chopped earthworm. Each sample was transferred to a wide-mouthed jar containing 500 c.c. of filtered pond water. Four cleaned worms were put into each jar and examined for *Urceolaria* after 5 days. The sampling was carried out four times, giving twenty substrate samples in all. Of these, seventeen proved negative, three positive. Of the latter, one sample had one worm infested with two *Urceolaria*, in another one worm had seven *Urceolaria*, while in the third a single worm carried one *Urceolaria*. It is probable that in the case of the flatworm with seven epizoites the latter had multiplied after becoming attached.

It must be concluded that *U. mitra* may occur on the substratum in small numbers and attach itself to flatworms as opportunity offers.

(c) *Duration*

It has been shown that *U. mitra* occurs in the plankton, probably in small numbers only. The efficacy of this method of dispersal depends also on the duration of free existence. To examine this, five *U. mitra* brushed from their host on to a cover-glass, were kept in 5 c.c. of pond water in a solid watch-glass. The experiment was set up in quadruplicate, providing twenty *Urceolaria* for observation. The condition of these was noted at 8 hr. intervals. After the

first period only five individuals were still alive, three actively swimming, two with the cilia still beating. The remainder were in various stages of disintegration. After 16 hr., only one showed any activity, the aboral and gullet cilia still beating. It remained active for 48 hr. Controls on flatworms were still alive.

To verify that the small volume of water in which they had been kept was not harmful, a further test was made using 250 c.c. of pond water. Five jars in three series were set up and five *Urceolaria* added to each. At daily intervals cleaned flatworms were added to one jar from each series and examined for *Urceolaria* after 24 hr. None was found after 1, 2 and 3 days, and on the fourth day all six jars remaining were 'baited' with negative results again. Thus out of seventy-five *Urceolaria* none was recovered, this agreeing with the results of direct observation. It must be concluded then that the duration of free existence is short, only from 1 to 8 hr.

This experiment also illustrates the dependence of *U. mitra* on its host. Since it is unlikely that the flatworm benefits from the association, on Carter's (1940) definition of parasitism, *U. mitra* is an 'ecto-parasite'. Alternatively, according to other workers (Kirby, 1941), it would be classed as an 'ecto-commensal'. The obvious advantages derived from the host are provision of transport and of a ciliary current in which to feed. The brief period of free existence and the marked host specificity (Reynoldson, 1950) suggest that there may be other more subtle links between *Urceolaria* and its host. Until its food has been determined and the relationship studied more closely, the non-committal description of 'epizoic' is being retained.

5. AN ANALYSIS OF DISPERSAL METHODS

U. mitra has been shown to occur in the plankton in small numbers under natural conditions (§4), and subsequent attachment to its host may result from chance contact or the operation of some taxis. But the aggregational behaviour of the host during periods of inactivity and the crowding which occurs during feeding afford ample opportunity for *Urceolaria* to spread by contact. So far it has not been determined whether *Urceolaria* uses both methods for dispersal or only one. Further, if it uses both, are they of equal importance? Experimentally it is difficult to test for dispersal by host contact while at the same time preventing the possibility of it occurring by free-swimming *Urceolaria*. Therefore an attempt to provide some answer has been made by indirect methods. In considering the following experiments it should be pointed out that populations of *Urceolaria* kept in filtered pond water at temperatures about 15° C. change little numerically in 3 days.

It is argued that if *Urceolaria* spreads frequently by becoming planktonic under laboratory conditions then free individuals should occur in the water, whereas if host contact is the only avenue then the epizoite should not occur free. Such a distinction is difficult to demonstrate, since the concentration as plankton is likely to be small (§4) and can only be shown by using large numbers. Therefore, ten infested flatworms were added to each of twenty vessels containing 150 c.c. of filtered pond water and left for 24 hr. at room temperature which fluctuated between 15 and 20° C. After their removal five cleaned flatworms were added and left for 8 hr. to attract free *Urceolaria*. It was considered better to remove the infested flatworms from the water rather than pour the water into another vessel and then test it. Observation had shown that on disturbance the *Urceolaria* tended to cling more tightly to their host while when free they often attached themselves to the substratum and would have been left behind in the vessel. The answer was quite definite, since twelve of the twenty tests gave a positive result, and out of 3400 *Urceolaria* used thirty-three became free-swimming—an average percentage of at least 0.97 with a range of 0.2.94 % in the individual experiments. If *Urceolaria* is continually leaving and re-attaching to its host, then using the data in Table 2 the dispersal rate can be set at 0.97 % per 6 hr. as an approximation. The number recorded from individual vessels ranged from nil to five, with an average of 1.65 *Urceolaria*. Thus it is quite certain that *Urceolaria* becomes planktonic under laboratory as well as natural conditions. But the relative importance of host contact as an additional means of dispersal remains obscure.

Observations on dispersal from infested to uninfested worms have been made many times for other purposes in varying volumes of water and in concentrations of the epizoite ranging from low (two *Urceolaria* per worm) to average densities (sixteen per worm). The technique used was to add ten cleaned, and five infested flatworms to the vessel containing filtered pond water, and then after 3 days to determine the number of *Urceolaria* on the originally uninfested and the infested worms. Ten such experiments were made, two at each of the following volumes of water, 10, 50, 250, 1000 and 5,000 c.c. under laboratory conditions similar to the previous experiments on the planktonic aspect. The total number of *Urceolaria* dispersing to the cleaned worms was thirty-nine, while the total remaining on the infested worms was 441. Neither the volume of water nor the concentration of *Urceolaria* seemed to influence the dispersal rate, although the concentration did not reach a high level by natural standards (Reynoldson, 1950). If certain assumptions are made, it is possible to determine whether the dispersal observed could

be accounted for entirely by a planktonic method. Thus, if it is assumed that the number of *Urceolaria* becoming free in unit time is a constant proportion of the total epizoic population and that the period of free existence is 6 hr. (§4c), then to provide for the observed dispersal the percentage becoming planktonic averaged 1.06 % with a range of 0.45–1.7 %. These figures are quite close to the 0.97 % determined earlier and show that the observed dispersal can be entirely accounted for by free-swimming *Urceolaria*.

Further support for this idea was obtained by testing for dispersal during the period of the flatworm's feeding. Five infested worms, dark in colour, and ten cleaned worms, light in colour, were allowed to feed on a small piece of earthworm measuring approximately 2 by 1 cm. During feeding the worms were tightly packed around the food and in close contact with one another for about 30 min. Examination of the cleaned worms, when feeding had finished and they had separated, revealed no *Urceolaria*. A similar negative result was obtained on repeating the experiment.

Following up the view that *Urceolaria* spreads mainly by becoming planktonic and contacting a new host, it is clear that dispersal would be much more efficient if the epizoite has some mechanism for detecting its host. In an attempt to demonstrate a taxis equal numbers of cleaned flatworms were exposed to the same number of *Urceolaria* in different volumes of water. Thus if there is no such mechanism, the chance of *Urceolaria* contacting its host would decline as the volume of water was increased. Ten *Urceolaria*, obtained by gently brushing from their host on to a cover-glass, were added to each of the following volumes of water 10, 50, 250, 1000 and 5000 c.c., each containing ten cleaned flatworms. The ratio of depth to surface area of water was kept approximately constant by using vessels of suitable dimensions. The number of *Urceolaria* attaching to the flatworms was determined after an 8 hr. period (repeated) and also after intervals of 6 and 4 hr. The results are recorded in Table 2.

Table 2. *Efficiency of Urceolaria in colonizing its host in different volumes of water. Two groups in the 8 hr. experiment*

Vol. of water (c.c.)	No. of <i>Urceolaria</i> attaching, out of ten				No. of flatworms infested			
	8 hr.		6 hr. 4 hr.		8 hr.		6 hr. 4 hr.	
10	9	10	8	6	7	4	6	5
50	5	8	7	3	3	3	6	3
250	9	8	4	4	4	3	3	2
1000	10	5	2	3	6	3	2	2
5000	6	10	0	2	4	3	0	2

the pond with the rim just above the surface. Flatworms less than 1 day old were measured and added to the dish. Their size was then recorded every 4 days over a period of 16 days. The experiment was done in duplicate with similar results which showed that newly hatched flatworms added approximately 0.5 mm. to their length each week over this period. The average size of fifty-two flatworms on hatching was 2.17 mm. with a s.d. of 0.483.

A special collection of small worms was made from the pond in April 1947, during the peak of their breeding season to determine, first, at what size they initially become infested, secondly, the relation between size and incidence, thirdly, the relation between size and the epizoic population. Sixty-seven worms, ranging in length from 2.0 to 7.0 mm. were examined and their peritrich population is recorded in Fig. 1*a, b*. The smallest worms, whose age may be taken as between 0 and 1½ weeks, were not infested, half the worms in the 3 mm. category were infested (approximate age 1–4 weeks), while 100% infestation occurred when they had reached a length of 4.0 mm. The absence of *U. mitra* on a few individual worms of larger size may have been due to chance or to the fact that some worms are 3.0 mm. long on hatching. It seems reasonable to conclude that the dispersal rate was such that one half of the young worms became infested within a period of 1–4 weeks. The data on the number of *Urceolaria* per flatworm show that by the time an average length of 4.0 mm. had been reached, growth of the epizoic population had reached a maximum and become relatively stable under existing conditions. This agrees well with observations from routine collections. A further experiment on these two aspects under less natural conditions, viz. keeping newly hatched and adult-infested worms in aquaria, gave results comparable to the field collection.

7. DISCUSSION

In this paper diverse methods of determining the mechanism and the rate of dispersal of *Urceolaria mitra* are described and they give answers which agree within reasonable limits. At the outset it was considered, on the basis of general observation and of Keiser's (1921) paper, that *Urceolaria* probably spread by contact between hosts, since flatworms show a high degree of aggregational behaviour. This view was supported by the small number of free-swimming individuals found in the pond and by the short duration of a free life which was possible (§4(*a*), (*c*)). But the demonstration that *Urceolaria* was able to locate its host with marked efficiency put the matter in a new light. As a result of the last experiment, in which water previously containing infested flatworms was shown to contain free *Urceolaria*, it is now believed that *Urceolaria* disperses mainly by becoming

planktonic. This view was gradually forced upon the writer and it has been shown that such a method is sufficient to account for dispersal observed in the laboratory. Further, it would also explain the persistence with which caged flatworms (§4(*a*)) become infested under otherwise natural conditions. The numerically small planktonic population is also sufficient to account for natural dispersal, since *Urceolaria* is able to find its host so readily. The duration of the free existence approximates to the average time taken for *Urceolaria* to locate its host. The relatively small incidence of free existence also explains why *Urceolaria* was not seen to leave its host on the many occasions when worms were observed. It is also probable that when worms are under observation the *Urceolaria* tend to remain attached.

It is possible to compare very approximately the size of the free-swimming population of the pond and that of the laboratory by a rather devious method. Thus, if it is assumed, as before, that the number of *Urceolaria* becoming free is a constant proportion of the total population (and this is probably true for middle-sized populations), then knowing the number of free *Urceolaria* per litre of pond water (§4(*a*)), the average urceolarian population per worm and the volume of water in the pond, it is possible to calculate the numbers of flatworms that occur. This has also been estimated approximately by other methods, and a comparison of the two will show whether the figure based on *Urceolaria* is reasonable or widely out. The actual number per worm during the estimate of the free *Urceolaria* was 20—a middle-sized population (Reynoldson, 1950). From these data it is calculated that the total population of *Polycelis tenuis* in the pond amounted to 25,000. In the previous paper this was estimated at not less than 20,000 and the figure of 25,000 is probably correct within $\pm 50\%$, which is a very reasonable result suggesting that the number of *Urceolaria* becoming planktonic under laboratory conditions reflects their natural behaviour. Thus there is conclusive evidence that Keiser was in error in thinking that *Urceolaria* did not occur free—in fact it depends on free-swimming individuals for dispersal to new hosts.

It would appear that *Urceolaria* leaves its host voluntarily. Something of the sort must also occur with *Trichodina* species, which are internal parasites. Mueller (1938) suggests that *Trichodina* may become free-swimming during the breeding season of its host *Esox niger* when the fish congregate. *Urceolaria* may also accidentally part from its host, while a proportion of the small planktonic population may originate from dead flatworms. Brouardel (1947) noted that *U. patellae* abandoned sickly limpets. It is not known whether the planktonic phase is seasonal or related to such factors as temperature, light or agitation of the water as Brouardel found for *U. patellae*. There is

some evidence that dispersal is greater when the epizoic population is high. Thus, in my paper discussing the population fluctuations of *U. mitra*, it is shown that the high degree of specificity for *Polycelis tenuis* breaks down temporarily when the peritrich reaches high levels of abundance. At such times it spreads on to *Dugesia lugubris*. Any factor such as overcrowding which may cause the epizoite to become more active on the surface of the worm may cause more rapid dispersal. The occupation of less favourable habitats, such as *D. lugubris* represents, during periods of population pressure is well known for other animals, particularly insects and mammals. It has been suggested as a factor in the control of the population and is discussed by Solomon (1949) in this connexion.

Brouardel's paper (1947) on dispersal in *Urceolaria patellae* living on the gills of limpets appeared when the work on *U. mitra* was half completed. Since we were both studying the same sort of problem it is not surprising that the approach was similar and the pattern of experiments only differed in relation to the different hosts. His work was more empirical and not so closely related to field conditions because the limpet population was more difficult to assess. On the other hand, it deals with larger numbers of the peritrich. The results of the two studies are closely similar, and the work on *U. mitra* confirms many of the conclusions which Brouardel reached for *U. patellae*. Thus he found that larvae of *Patella* were not infested and after their settlement infestation had to come from an outside source, just as in flatworms. He also showed that the free existence of *U. patellae* was short, the peritrichs dying after 6–8 hr., although some individuals lived longer. His results differed in one respect—by exposing limpets to free-swimming *Urceolaria* he found that they became infested but at a slower rate than when host contact was permitted. He did not determine whether any taxis was involved. He was also of the opinion that *U. patellae* rarely left the limpet gills voluntarily and as a result they occurred in natural waters only in small numbers. But he did observe infrequent excursions from the host which were not seen with *U. mitra*, but it must be remembered that each limpet was infested with thousands of *U. patellae*. This brief summary of Brouardel's paper shows the close

similarity in the behaviour and dispersal of these two urceolarians.

8. ACKNOWLEDGEMENTS

I am indebted to Prof. F. W. Rogers Brambell, F.R.S., for his interest in this work and his helpful criticism of the manuscript.

9. SUMMARY

1. The dispersal of *Urceolaria mitra* von Sieb epizoic on flatworms (*Polycelis tenuis* Ijima) has been studied by laboratory and field experiments.

2. The life cycle of the peritrich is not complicated by resting stages. Newly hatched flatworms are not infested; this occurs from outside sources.

3. In one series of experiments dispersal in small volumes of water from infested to uninfested adults and the establishment of an equivalent population took about 4 days—spread to newly hatched worms took longer.

4. Contrary to former opinion *Urceolaria* occurs naturally in the plankton and on the substratum in small numbers. It is only able to exist apart from its host for a short period, approximately 6 hr. It will also become planktonic under laboratory conditions, but infrequently. It is able to locate its host efficiently and can do so within 6 hr. in a relatively large volume of water.

5. Experiment has suggested that dispersal occurs mainly by *Urceolaria* becoming free-swimming and finding a new host. Such a method accounts for the dispersal observed in the laboratory.

6. No dispersal was observed when worms were crowded during feeding.

7. By measuring the growth rate of young *Polycelis tenuis* and determining the incidence and abundance of *Urceolaria mitra* in collections of small worms it has been calculated that half of the newly hatching worms become infested in 1–4 weeks. The peritrich population reaches an average maximum when the worms have reached 4.0 mm. in length.

8. The dispersal behaviour and duration of free existence of *U. mitra* is very similar to that of *U. patellae* from limpets.

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THE BOTTOM FAUNA OFF THE SOUTH OF THE ISLE OF MAN

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(With 1 Figure in the Text)

CONTENTS

	PAGE		PAGE
1. INTRODUCTION	132	7. QUANTITATIVE RESULTS	139
2. METHODS	132	8. SUMMARY	141
3. THE AREA INVESTIGATED	133	REFERENCES	141
4. HYDROGRAPHICAL CONDITIONS	134	APPENDIX: PERCENTAGE OCCURRENCE OF	
5. THE ANIMAL COMMUNITIES	135	SPECIES ON DIFFERENT GROUNDS	142
6. COMPARISON WITH OTHER AREAS	138		

1. INTRODUCTION

These investigations were undertaken to provide better information about the distribution of the benthos within working distance of the Marine Biological Station, Port Erin. Previously only the area within about 2 miles radius of Port Erin Bay had been systematically explored (Jones, 1940) and records from further afield have been few. It is essential that workers at a biological station should know where to find the animals they require without much searching, and for reference a typescript has been prepared and deposited in the library at Port Erin showing for each species obtained during this survey the number of specimens in each haul, together with details of position, depth, and type of gear used. These records will eventually be incorporated in a new edition of *The Marine Fauna of the Isle of Man*.

A start was made during the summer of 1946, when the 39 ft. fishing vessel, *Glee Maiden*, was hired for a series of exploratory excursions. In the following summer, 1947, the work was extended and quantitative investigations with a bottom-sampler were introduced. In 1948 the Biological Station acquired the 61½ ft. M.F.V. *William Herdman*, which started operating in September. The survey was continued at intervals from that date until April 1950.

During 1946 and 1947 the survey was confined within a radius of about 10 miles from Port Erin, and could be undertaken only during the summer and autumn months, but during 1948-9 the availability of a larger vessel allowed the range to be increased, and work continued during the winter and spring. The final limits decided on were within 15 miles from Port St Mary, that being the greatest distance to which the ship could run and return within one day and at the same time allow a reasonable amount of

time for work. Not all of this area has been equally well explored, but enough has been accomplished to decide the approximate limits of the various types of ground included.

I am much indebted to Prof. J. H. Orton, F.R.S., who made possible the early part of this work, and to the crews of the *Glee Maiden* and *William Herdman* for their assistance in the collections at sea.

2. METHODS

To a great extent the success of an exploratory faunal survey in any area depends upon the gear and methods used. Different types of gear must be used on different grounds and for different purposes. By using a variety of gear it may be ensured that the collections include the great majority of the species present. At the same time it is impossible for a single worker to deal adequately with every animal group. I have attempted to cover as wide a field as possible, but observations are confined to the larger animals, such forms as Protozoa, Platyhelminthes, Nematoda, and the smaller Crustacea including Copepoda and Ostracoda, being omitted, while records of Porifera, Hydroida, Polyzoa, and Tunicata are incomplete. Only such fish as were caught in dredges are included. The remaining groups have been fairly well covered, but records are not always complete for every haul as special treatment involving much time is necessary to obtain many of the smaller animals. Southern (1915, pp. 93-5) gives an interesting example of special treatment: by stirring up the contents of a dredge haul and filtering the water through silk, many species, particularly of Nematoda, Polychaeta, and small Crustacea new to the British fauna or previously undescribed, were found. In the majority of hauls, other than those with the bottom-sampler, only the larger animals have been noted, and in some

cases only a sample of these. In all, 134 grab samples and 111 hauls with other instruments were taken. It is inevitable that as a result of such a survey many new records will be obtained, and the fauna list for the area has been considerably augmented. Upwards of 527 species were identified, of which 75 are new to the fauna of the Isle of Man. However, in spite of these additions, it must not be assumed that the distribution of any group of animals in the area is now thoroughly known. A step in this direction has been taken in the case of the Amphipoda (Jones, 1948), but each group requires treatment by itself. In particular the records of the Polychaeta are probably still deficient.

Instruments used for collecting include the following:

(1) Various otter trawls, particularly a small heavy type adapted for catching bottom animals. These trawls are useful for covering a larger area than other catching instruments, but retain only comparatively large animals. A 5 ft. Agassiz trawl was used on a few occasions on soft ground.

(2) Various dredges both of the oyster and naturalist's type. For a description of the former, which was always used with an inner lining of shrimp netting, see Davis (1927). These instruments are the most generally useful for exploration, particularly on rough ground. In addition, it has been found valuable to use a naturalist's dredge with the frame bowed out so that it digs into the substratum. With a canvas bag attached a fair sample of the bottom deposit and the animals contained in it may be brought up even on rough ground.

(3) A 0.1 m.² bottom-sampler. This is of the van Veen type, described by Thamdrup (1938), consisting of a grab which closes through the leverage of long arms to which the bridles are attached. It was used for quantitative work and for determining the extent of the softer grounds. On mud and muddy sand no difficulty was experienced in obtaining good samples. On fine sand only the top few centimetres is scraped, while on gravels and coarse grounds other than fine shell-gravel it is almost useless. This defect, unfortunately, is common to all types of bottom-sampler so far devised, with the result that accurate quantitative work cannot be carried out on the coarser grounds.

(4) Miscellaneous gear. On two occasions a Petersen young fish trawl was being used and came up full of mud, having been dragged for some distance along the bottom. Such usage is not recommended as normal practice, but can provide a useful collection of animals living close to the bottom. For routine work on such lines a runner-dredge as described by Elofson (1941) was constructed, and a number of hauls have been made with it. A most useful method of obtaining small species that are difficult to get by other means is to attach cut-away tow-nets to the back of an otter

trawl. Some of the animals stirred up by the foot-rope and which normally pass through the meshes of the trawl are retained by this means (see Kemp, Hardy & Mackintosh, 1929).

In the case of the trawl and dredge hauls the whole of the contents was sometimes taken back to the laboratory and thoroughly searched for animals, this being the only method of ensuring that the smaller forms were found, and necessary in the case of fine-meshed dredges. As a rule, however, the animals were sorted out on board and the remainder thrown back, notes being made at the time of the nature of the bottom deposit. In the early part of the work samples taken with the grab were brought in and the animals obtained by sieving the deposits, but later the samples were washed through a sieve by means of a hose on board. In all cases the sieve used had holes of 1 mm. diameter.

It was not thought necessary to grade the deposits by weighing the various grades of particles, as after a little practice a sufficiently distinctive description for the purpose in view could be given after feeling and examining them. Positions of hauls were fixed by means of cross-bearings on landmarks or, in the few cases when visibility was too poor, by dead reckoning.

I am personally responsible for all identifications.

3. THE AREA INVESTIGATED

Except in the bays, the coast is fairly steep along the south-west of the Isle of Man and the water deepens rapidly to about 10 fm. The slope is then gradual to the 50 fm. line about 10 miles offshore. Between the Isle of Man and the Irish coast is situated a deep channel in which soundings reach over 70 fm. The tidal range is from 15 to 20 ft. during springs. In the bays the slope close to the shore is more gradual. Off the south and east coasts of the Island the bottom, though irregular in places, slopes downwards more gradually, and between the Isle of Man and the Cumberland coast depths of more than 20 fm. are present in only a few places.

All the grounds found to occur in the area fall more or less into four divisions, according to grade of particles:

- (a) Coarse sands, gravels including shell, and stony grounds.
- (b) Fine sand.
- (c) Muddy sand.
- (d) Mud.

The main factors controlling the distribution of the various grades of deposit are the strength of the tidal current (see p. 135) and wave action. Where the tide runs strongly the finer particles are swept away, leaving only gravels and stones. In the larger bays and inlets of the coast where the tidal currents are slowed down, wave action prevents the accumulation

of mud but allows fine sand to remain. The only places in which mud accumulates on the foreshore are in Port St Mary Harbour and Derbyhaven, both of which are very sheltered from prevailing winds by their natural topography and by the presence of breakwaters. Outside the fine sand or gravel areas is a belt of muddy sand where tidal action is less strong but wave action still prevents the accumulation of much mud. In deeper water, where both tides and wave action are weak at the bottom, deposits of sticky mud occur.

The approximate limits of the various grounds are shown in Fig. 1. It must not be supposed that the division between them is abrupt; on the contrary there is usually a gradual change from one ground to another, but this transition zone is of small extent compared with the area that can definitely be allotted to one ground or another.

(a) The gravel and shell grounds

The largest area of coarse ground extends from the south side of Port Erin Bay in a wide arc west and south of the Calf and extending to a considerable distance south of Douglas and up the east coast to Maughold Head. The southern and eastern boundaries have not been determined. Close in to the land the deposit is largely gravel and stones, probably augmented by landslides where the cliffs are steep. Where tidal action is at its strongest, as just south of the Calf and round the Chicken Rock, off Spanish Head, Scarlet Point, and Langness, the deposit is composed of larger stones and there may possibly be rock outcrops. The area west and south of the Chicken Rock has a bottom of coarse sand and gravel with a considerable cover of dead shells and shell fragments. The shells are largely those of *Glycimeris glycimeris*. Towards the western and south-western boundaries of the ground the amount of coarse material decreases. The deposits to the south and east of the area, as far as ascertained, consist of coarse sand, gravel and stones, with a fair amount of broken shell. About 1½ miles south of Spanish Head, on the Warts Bank, occurs a considerable deposit of shell-gravel, consisting mainly of calcareous material. This deposit becomes finer towards the west, ending as coarse sand just off the Burrow on the Calf. It seems to be deposited where the strong tide through the Sound slackens.

South and south-west of Niarbyl there occur extensive deposits of coralline algae, *Lithothamnion* sp., lying on and among the gravel. Similar deposits occur south-east of Port St Mary and for about 1-2 miles off the coast north-east of Langness, extending to greater distances south-east and east of Douglas Head.

At its deepest the gravel and shell ground extends to about 35 fm.

(b) The fine sand ground

Fine sand in the area investigated is confined to the following bays: Port Erin Bay to a little beyond Bradda Head, Baie-ny-Carrickey to a little below low water springs, Castletown Bay, Derbyhaven, Fleshwick Bay with a tongue extending about 1 mile south-west and 2 miles north-west, and a small area just north of Niarbyl Point.

(c) The muddy sand ground

To the west and south-west of the area the gravel and shell and the fine sand grounds grade into muddy sand. The deposit approaches the coast much more closely off the west coast where tidal action is weaker than to the south. In deeper water it grades rather gradually into the mud.

In the shallower parts the deposit contains a good deal of coarse material mixed with or lying on the muddy sand, in particular pieces of broken shell, largely *Pecten maximus*. The amount of shell decreases gradually down to about 35 fm. in the south-west and 20 fm. in the north-west of the area. Lying with its centre about 9 miles west of Port Erin is the Traine Bank, which rises to about 26 fm. from greater depths surrounding it. The deposit on this bank is somewhat coarser than that on the neighbouring deeper bottom. At one place roughly 7 miles south-west of the Chicken Rock the deposit contains large lumps of firm clay.

(d) The mud ground

At a distance of about 10 miles off the coast to the south-west in 35-40 fm., but approaching to about 5½ miles off Glen Meay farther north in about 28 fm., the muddy sand grades into a sticky mud which occupies the deep channel lying between the Isle of Man and Ireland. Soundings down to about 75 fm. occur. In the shallower parts the mud contains numbers of empty shells of *Turritella communis*. The only coarse material in the deeper parts is clinker dropped by ships.

4. HYDROGRAPHICAL CONDITIONS

(a) Wave action

The sea area off the south of the Isle of Man is fairly exposed and the prevailing winds are south-westerly. Although from its position in the middle of the Irish Sea the Isle of Man is not subjected to the full force of the Atlantic swell, gales are of frequent occurrence, particularly in the winter, and in all but the most sheltered bays wave action exerts its effect. It is probably felt on occasions down to a depth of about 25 fm., that being the least depth at which the mud is found.

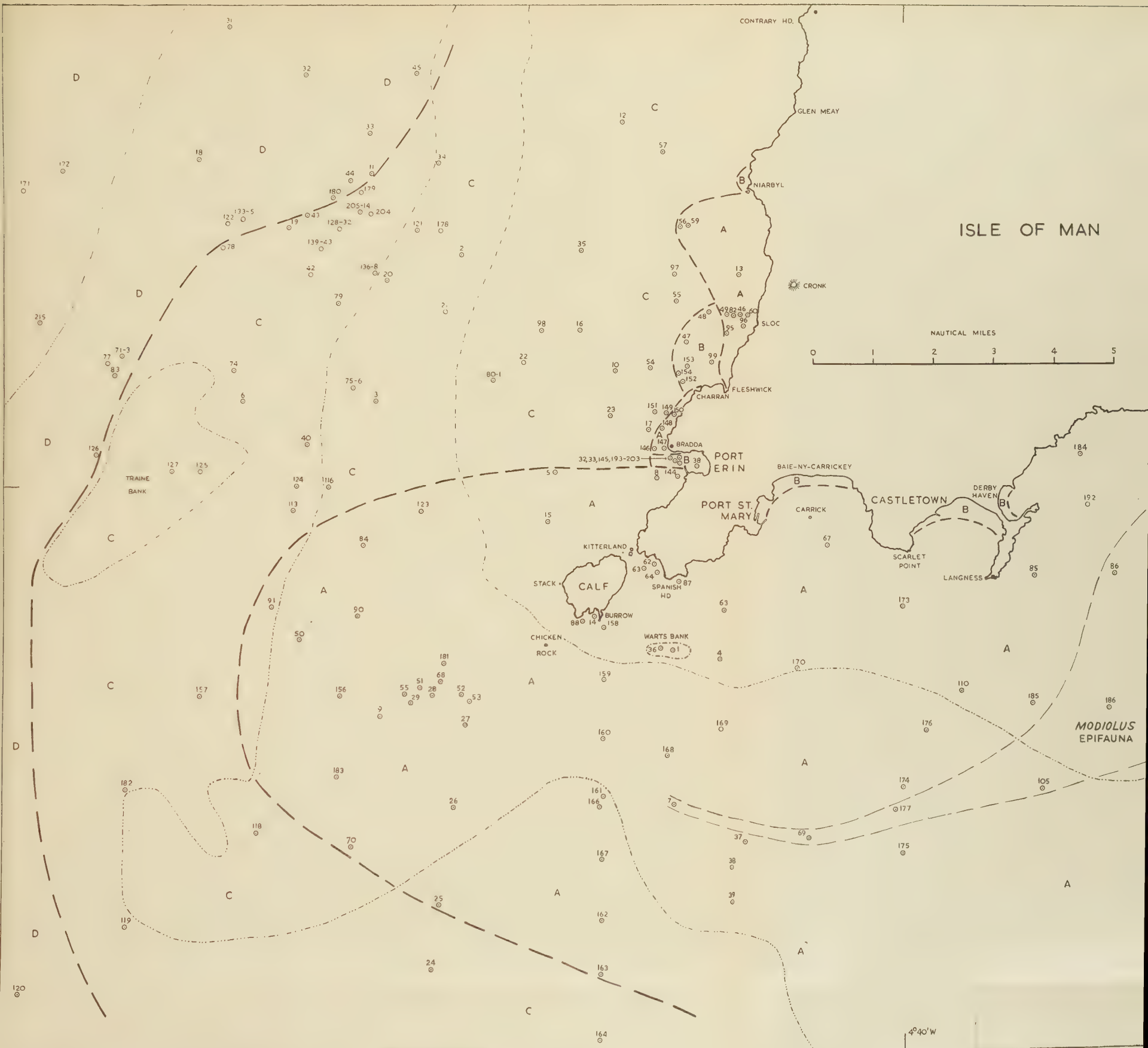


Fig. 1. Map of the sea area off the south of the Isle of Man, showing positions of hauls and approximate boundaries of grounds. $\odot$, positions of hauls. —, boundaries between grounds; A, fine sand; B, fine sand; C, muddy sand; D, mud. —, 10 fm. line; - - -, 20 fm. line; ·····, 30 fm. line; ······, 50 fm. line.

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(b) Tides

The set of the tides round the Isle of Man is made up of components from St George's Channel and the North Channel. During the flood along the west coast the North Channel component divides off Contrary Head, one branch passing along the north-west coast and round the Point of Ayre, the other passing south round the Calf and through the Sound. Off the Calf the south-going stream joins the component from St George's Channel, both streams then moving eastward along the south coast. The ebb is in the reverse direction. The rate off Contrary Head is about 1 knot during spring tides about 3 hr. before high water at Liverpool, increasing as the stream moves south. The north-going component approaches 2 knots at spring tides south-west of the Calf, and the combined streams reach more than $4\frac{1}{2}$ knots along the south-east coast off Langness, decreasing as they move eastwards. There is a large area with its centre about 25 miles WSW. of the Calf where no appreciable stream is felt. The rate is strongest close to the shore past exposed headlands, the stream taking the shortest route from one to another with the result that it is very much lessened in the bays. It decreases off-shore in greater depths (see *West Coast of England Pilot*, Admiralty, 1948).

It is therefore close to exposed headlands, and particularly in a large area west of the Calf and off the south-east coast, that the coarser bottom-deposits occur.

(c) Temperature

The temperature of the waters of the Irish Sea has been the subject of a paper by Matthews (1914) and that of the surface waters by Proudman, Lewis & Dennis (1937). The mean surface temperature in the area varies between 6.5 and 7.5°C . in February and 13.5 and 14.5°C . in August. The mean range is greatest at the eastern edge. In February the bottom temperature at 50 fm. in the south-west of the area is practically identical with that at the surface, namely about 7.5° according to Matthews. In May the bottom temperature is still about 7.5° but the surface is warming up and reaches about 8.5° . In August the bottom temperature has increased to about 11.5° while the surface temperature reaches about 13.5° . In November the temperature is again uniform throughout the water layer at about 12.0° . The mean temperature at 50 fm. therefore varies from about 7.5° in May to about 12° in November. The reasons for the uniformity in temperature throughout the water layers from November to February may probably be found in the prevalence of winter gales, which cause thorough mixing.

Temperature observations taken during the present survey confirm those of Matthews. No regular hydrographic series was undertaken, but occasional

readings using a Nansen-Petterssen water bottle showed temperatures within the range indicated above.

(d) Salinity

The mean salinity in the area varies from about 34.25‰ at the surface in February to 34.07‰ in August (Matthews, 1914). In February the salinity is uniform throughout the water layers, showing a slight increase with depth as the summer progresses, amounting to 0.1‰ difference between the surface and bottom at 50 fm., and becoming uniform again in November. There is thus little change in salinity between surface and bottom, and little seasonal variation, the mean surface value for the whole year in the area being between 34.2 and 34.1‰ , the decrease being in an easterly direction (Proudman, 1946).

Observations during 1946 (titrations kindly carried out by Mr J. R. Bruce) show bottom salinities at depths from 30 to 48 fm. ranging between 34.07 and 34.16‰ in August and September. In August 1948, bottom salinities in the same area at depths from 15 to 42 fm. ranged between 33.87 and 33.92‰ . In April 1949, bottom salinities at depths from 20 to 65 fm. ranged between 33.86 and 34.08‰ . In each case the highest value was obtained at the greatest depth. There appears to have been a significant difference between the values for August 1946 and those for August 1948, possibly indicating a decreased flow through St George's Channel during 1948, when the salinities are lower than the surface mean calculated by Proudman. The differences are almost certainly too slight to have any direct effect upon the benthos, though there may have been some change in the composition of the plankton.

5. THE ANIMAL COMMUNITIES

The fauna of the sea bottom off the south of the Isle of Man falls into four groups correlated with the different types of bottom deposit. Each group may be considered as a community on the lines first brought into prominence by C. G. J. Petersen. The latter distinguished two series of animals living side by side—the infauna, consisting of those which burrow into or live among the deposits of the level sea bottom, and the epifauna, including species that are fixed to the surface of the substratum as objects upon it and wandering species which move more or less actively over the surface. The distinction between the two is by no means always clear, and both infauna and epifauna must be regarded as components of the same community, but the term is useful descriptively.

The Appendix shows the percentage occurrence of species on different grounds for all hauls in which animals were identified during the course of the survey. The large numbers of hauls taken and species

identified would occupy too much space if each haul were shown separately in tabular form. Therefore species that were obtained in less than 10% of the hauls have been omitted and it was thought best to present the results as set out in the Appendix for the following reasons. The number of hauls taken on the different grounds varied considerably. Only the bottom-sampler hauls are comparable as regards numbers of individuals; those taken with other instruments, which necessarily included nearly all on the gravel and shell ground, cannot be compared one with another or with the grab hauls. In some cases several separate hauls were recorded as one. If occurrence only is used the differences between the area covered by different instruments is minimized, and expressed as a percentage of the total possible occurrence on each ground the figures may be used to compare the distribution of the animals throughout the area. Finally an analysis of the distribution of the fauna based on the Appendix shows no important differences from one based on full tables showing the numbers of each species per haul.

The communities will be named according to the scheme outlined by Jones (1950), i.e. they are named after the deposit on which they occur. Since other physical conditions, e.g. temperature and salinity, are almost uniform offshore throughout the area at any given time, the nature of the bottom deposit and the correlated maximum amount of water movement are the only significant variable factors. As with the deposits, the communities are not discontinuous and, apart from the widely distributed species which are common to several, there is an actual overlapping at the boundaries where one deposit changes gradually into another. Nevertheless, this does not prevent the main communities from being distinct from one another.

The fauna throughout each community area is not quite uniform. For example there are certain differences between the fauna of the finer gravels and that of the coarser deposits, while the shallower parts of the muddy sand community area contain a number of species absent from the deeper parts, but it has not been found possible to make any subdivisions on this basis because the differences are largely quantitative rather than qualitative. These differences will be shown under the relevant communities. An attempt might have been made at division into separate facies, but in my opinion it would be difficult to justify.

The offshore bottom fauna therefore falls into the following main communities:

- (a) The offshore gravel community.
- (b) The offshore fine sand community.
- (c) The offshore muddy sand community.
- (d) The offshore mud community.

Each community occurs in the area described under the respective grounds.

(a) The offshore gravel community

The fauna common to the whole area includes the following important species:

POLYCHAETA: *Lepidonotus squamatus*, *Pomatoceros triqueter*; CRUSTACEA: *Galathea intermedia*, *Eupagurus bernhardus*, *Ebalia tuberosa*; MOLLUSCA: *Glycimeris glycimeris*, *Modiolus modiolus*, *Chlamys opercularis*, *Lima loscombi*, *Venus casina*, *V. fasciata*, *Calliostoma zyziphinum*, *Buccinum undatum*; ECHINODERMATA: *Solaster papposus*, *Henricia sanguinolenta*, *Asterias rubens*, *Ophiothrix fragilis*, *Ophiocomina nigra*, *Psammechinus miliaris*, *Echinus esculentus*, *Spatangus purpureus*.

Of lesser importance but widespread are:

CRUSTACEA: *Pandalus montagui*, *Porcellana longicornis*, *Inachus dorsettensis*; MOLLUSCA: *Pecten maximus*, *Chlamys tigrina*, *Astarte sulcata*, *Paphia rhomboidea*, *Gari tellinella*; ECHINODERMATA: *Ophiopholis aculeata*, *Ophiura albida*.

Other species are found more locally, some being absent from the finer gravels and others being found only in these deposits. As all the deposits in the area occupied by this community are subjected to some current or wave action it is evident that the fauna of the finer gravels will be poorer in species than that of the coarser gravel and shell deposits, since many species will be unable to withstand the greater amount of movement among the finer particles. This applies particularly to fixed animals. These may be unable to find anchorage on small particles unless they have a rooting system, or they may be rubbed off by the grinding together of the particles. The observed distribution of the fauna bears out this contention. Fixed species find the most favourable habitat on the coarsest deposits, large stones or even rock outcrops, and since these are covered by finer particles except where there is considerable water movement, the animals on them are further favoured by an abundant supply of food organisms. Many species dependent on the fixed animals for food or shelter are found with them on the coarse deposits. On the other hand, some burrowing animals find conditions unfavourable among large particles.

Important species found particularly in the finer deposits, coarse sands, fine gravels, shell-gravels, and corallines, include:

ARCHIANNELIDA: *Polygordius lacteus*; POLYCHAETA: *Glycera lapidum*, *Lumbriconereis impatiens*, *Pista cristata*; CRUSTACEA: *Conilera cylindracea*, *Eurydice inermis*, *Metaphoxus fultoni*, *Ceradocus semiserratus*; *Portunus pusillus*; MOLLUSCA: *Nucula hanleyi*, *Spisula elliptica*, *Thracia villosiuscula*, *Gibbula magus*, *Gibbula tumida*; ECHINODERMATA: *Amphiura securigera*, *Echinocyamus pusillus*.

These are nearly all burrowing species.

The following occur mainly on the coarser deposits,

coarser gravels mixed with finer particles, dead shells, and stones:

COELENTERATA: *Abietinaria abietina*, *Hydrallmania falcata*, *Sertularia argentea*; POLYCHAETA: *Serpula vermicularis*, *Hydroides norvegica*; CRUSTACEA: *Balanus porcatus*, *Spirontocaris pusiola*, *Eupagurus prideauxi*, *E. pubescens*, *Hyas coarctatus*, *Macropodia longirostris*; MOLLUSCA: *Lepidopleurus asellus*, *Monia squama*, *Emarginula reticulata*; POLYZOA: *Flustra foliacea*. All these species are epifaunistic.

Finally a number of species are restricted more or less to certain localities, in some cases without any very obvious reason. *Modiolus modiolus* occurs in small numbers throughout the area of this community except on the very finest gravels and coarse sands, but it is found abundantly off the south-east coast. Here it forms in places a solid mass of shells on the bottom, the animals attached to one another by byssus threads. The bed of *Modiolus* commences as a narrow strip less than $\frac{1}{4}$ mile in width about 4 miles SSE. of the Calf in 30 fm., and runs in an arc to about the same distance offshore to the south of Langness about the 20 fm. line. From here the bed broadens out considerably, becoming 3–4 miles in width, but with the *Modiolus* much less concentrated than in the western part, and finishes from 3 to 7 miles south of Douglas Head in 16–22 fm. The bed seems to be outside the course of the strongest tidal currents, which run close to the Calf and to Langness, but in an area where there is still considerable water movement.

Associated with the *Modiolus* is a typical fauna, including the following species:

Sponges, particularly *Desmacidon fruticosum*; the hydroids *Abietinaria abietina* and *Sertularia argentea*; POLYCHAETA: *Lepidonotus squamatus*; *Syllis spongicola* in the sponges; *Nereis pelagica*; *Serpula vermicularis*, *Pomatoceros triqueter* and *Filograna implexa* growing on the *Modiolus* shells; CRUSTACEA: *Balanus porcatus* and *B. hameri*; *Perrierella audouiniana* and *Leucothoe spinicarpa* in the sponges; *Pandulus montagui*, *Galathea intermedia*, *G. nexa*, *Porcellana longicornis*, *Eupagurus bernhardus*, *E. pubescens*, *Ebalia tuberosa*, *Xantho couchi*, *Eurynome aspera*, *Pisa gibbsi*, *Hyas coarctatus*, *Macropodia longirostris*; MOLLUSCA: *Glycimeris glycimeris*, *Monia squama*, *Chlamys varia*, *C. distorta*, *C. opercularis*, *Venus casina*, *Calliostoma zyziphinum*, *Buccinum undatum*; ECHINODERMATA: *Solaster papposus*, *Henricia sanguinolenta*, *Asterias rubens*, *Ophiothrix fragilis*, *Ophiocomina nigra*, *Ophiopholis aculeata*, *Psammochinus miliaris*, *Echinus esculentus*, *Spatangus purpureus*; various TUNICATA, particularly *Ascidia mentula*.

Most of these species are widely distributed on the gravel and shell grounds, but many are found more abundantly with the *Modiolus*, while at least one, *Balanus hameri*, does not seem to occur elsewhere in the area. Living on the shells of the *Modiolus* are

also occasional specimens of the gastropod *Capulus ungaricus*, while the small crab *Pinnotheres pisum* frequently inhabits the mantle cavity. The richness of this fauna is presumably due to the good anchorage afforded by the *Modiolus* for fixed organisms which provide food and shelter for other animals, while these in turn provide a food supply for predators.

In an area of several square miles centred about 3 miles south-west of the Calf, the bottom is overlaid by a deposit of dead shells, chiefly those of *Glycimeris glycimeris*. A number of animals seem to find this deposit particularly favourable. The solitary coral *Paracyathus taxilianus* grows on some of the larger pieces of shell, and the brachiopods *Terebratula retusa* and *Crania anomala* are locally common in the same habitat. *Lima loscombi* is particularly abundant, inhabiting nests made of shell fragments bound together by byssus threads, and in the nests the polychaete *Flabelligera affinis* is frequently to be found, perhaps living commensally with the lamellibranch. The small gobies *Lebetus scorpioides* and *L. orca* have been obtained on several occasions, the latter nowhere else within the area worked. Most of the shells are bored by the sponge *Cliona celata*.

The two ophiuroids *Ophiothrix fragilis* and *Ophiocomina nigra* occur in some places in enormous numbers, and as far as can be judged by dredge hauls must sometimes completely cover the bottom. *Ophiothrix* is usually the commoner, and sometimes occurs alone, but *Ophiocomina* is usually present in smaller numbers. On the other hand, *Ophiocomina* is occasionally present to the exclusion of *Ophiothrix*. The conditions that favour the presence of one or the other species have not been determined, but *Ophiothrix* seems to prefer rather deeper water and cleaner ground, while *Ophiocomina* is more abundant close to the coast or where there is less water movement.

(b) The offshore fine sand community

The fine sand fauna has been investigated in detail only in and at the entrance to Port Erin Bay. It is restricted in its distribution in the area and presumably is similar in the other bays where fine sand deposits occur.

The following are among the important species:

POLYCHAETA: *Harmothoe lunulata* (probably associated with *Echinocardium cordatum*), *Sthenelais limicola*, *Nephtys* spp., *Owenia fusiformis*, *Pectinaria koreni*; CRUSTACEA: *Iphinoë trispinosa*, *Ampelisca brevicornis*, *Bathyporeia guilliamsoniana*; MOLLUSCA: *Montacuta ferruginosa* (probably associated with *Echinocardium*), *Dosinia lupinus*, *Venus striatula*, *Gari fervensis*, *Tellina fabula*, *Abra prismatica*, *Cultellus pellucidus*, *Ensis ensis*, *Natica poliana*; ECHINODERMATA: *Amphiura filiformis*, *Ophiura albidula*, *Echinocardium cordatum*. Occasional specimens of

the crab *Corystes cassivelaunus* and the bivalve *Astropecten irregularis* occur, while *Crangon vulgaris* is common close inshore.

Most of these species are adapted to burrowing into sand. There is very little real epifauna, owing to the absence of suitable objects for fixation. The fauna in general is poor and shows no features of special interest.

(c) *The offshore muddy sand community*

This community shows a certain amount of gradation from the shallower deposits outwards towards the mud in deeper water, probably correlated with the decreasing amount of coarse material in the deposit. However, a sufficient number of species is common to the whole to characterize the community and it is not possible to make any satisfactory subdivisions.

The following are probably the most important species found throughout the community area;

POLYCHAETA: *Nephtys incisa*, *Goniada maculata*, *Lumbriconereis impatiens*, *Scalibregma inflatum*, *Owenia fusiformis*, *Amphiteis gunneri*; CRUSTACEA: *Ampelisca spinipes*, *A. tenuicornis*, *Lembos longipes*; MOLLUSCA: *Abra prismatica*, *Cultellus pellucidus*, *Aloidis gibba*; ECHINODERMATA: *Amphiura filiformis*.

Of lesser importance are:

POLYCHAETA: *Arabella iricolor*, *Diplocirrus glaucus*, *Pectinaria auricoma*, *Terebellides stroemi*; GEPHYREA: *Phascolion strombi*; CRUSTACEA: *Iphinoë serrata*, *Scopelocheirus crenatus*, *Harpinia pectinata*, *Eupagurus prideauxi*; MOLLUSCA: *Dosinia lupinus*; ECHINODERMATA: *Leptosynapta inhaerens*.

Species found more abundantly where there is some admixture of coarse material, gravel or shell, include:

POLYCHAETA: *Glycera convoluta*, *Pista cristata*; CRUSTACEA: *Ampelisca diadema*, *Urothoe elegans*; MOLLUSCA: *Dentalium entalis*, *Aporrhais pes-pellicani*; ECHINODERMATA: *Echinocyamus pusillus*, *Echinocardium flavescens*.

Where coarser material is mixed with the muddy sand or where shells or other objects overlie it there is also a sparse cover of the following, more properly belonging to the gravel and shell community:

POLYCHAETA: *Lepidonotus squamatus*, *Syllis armillaris*; CRUSTACEA: *Scalpellum scalpellum*, *Cressa dubia*, *Maera othonis*, *Phtisica marina*, *Galathea intermedia*, *G. dispersa*, *Ebalia tuberosa*; MOLLUSCA: *Pecten maximus*, *Chlamys opercularis*, *C. striata*, *Astarte sulcata*, *Venus ovata*, *Natica poliana*; POLYZOA: *Cellaria fistulosa*; ECHINODERMATA: *Solaster papposus*, *Asterias rubens*, *Ophiocoma nigra*, *Ophiura albida*, *Psammechinus miliaris*; TUNICATA: *Molgula occulta*.

Species found in greater numbers towards the mud deposits where coarser particles are lacking include:

POLYCHAETA: *Glycera rouxi*, *Prionospio cirrifera*, *Notomastus latericeus*; CRUSTACEA: *Diastylis lucifera*, *Alpheus ruber*; MOLLUSCA: *Nucula sulcata*, *Lima subauriculata*, *Mysia undata*, *Thracia phaseolina*, *Turritella communis*; ECHINODERMATA: *Brissopsis lyrifera*.

The finer grades of deposit are richer in species and individuals of the infauna than the coarser grades, but they have a very much reduced epifauna, among which the following occasionally occur:

COELENTERATA: *Thecocarpus myriophyllum*; POLYCHAETA: *Aphrodite aculeata*; CRUSTACEA: *Eupagurus prideauxi*, *Anapagurus laevis*; MOLLUSCA: *Chlamys opercularis*.

(d) *The offshore mud community*

The mud fauna contains fewer species than that of the other grounds. Owing to the nature of the deposit a fixed epifauna is virtually absent.

The following are the most important animals of the infauna:

POLYCHAETA: *Nephtys incisa*, *Glycera rouxi*, *Lumbriconereis impatiens*, *Notomastus latericeus*; CRUSTACEA: *Leucon nasica*, *Eudorella emarginata*, *Harpinia crenulata*, *Calocaris macandreae*; MOLLUSCA: *Nucula sulcata*, *Abra prismatica*; ECHINODERMATA: *Brissopsis lyrifera*.

Less important are:

POLYCHAETA: *Oxydromus propinquus*, *Diplocirrus glaucus*, *Scalibregma inflatum*, *Ammotrypane aulogaster*; CRUSTACEA: *Harpinia pectinata*, *Eusirus longipes*.

In addition on or close to the bottom in this community area and extending inwards over the outer part of the muddy sand the following active species occur among others:

CRUSTACEA: *Erythrops serrata*, *Pseudomma affine*, *Meganocyttaphanes norvegica* (Sars), *Pasiphaë sivado* (Risso), *Pandalus montagui*, *P. bonnieri*, *Processa canaliculata*, *Crangon allmanni*, *Philoceras echinulatus*, *Nephrops norvegicus*—very abundant in places; MOLLUSCA: *Sepiolo atlantica*, and the cephalopod *Alloteuthis subulata* (Lamarck).

Points of interest in the mud community are the presence of one or more specimens of *Calocaris* in almost every grab haul, showing its wide distribution in the mud, and the occurrence of numbers of Kinorhyncha—*Pycnophyes* spp.

6. COMPARISON WITH OTHER AREAS

The fauna of the area shows a considerable similarity, at least as regards the more important species, with those on similar grounds at other places within the Atlantic boreal region, e.g. Plymouth (Ford, 1923)

Table 1. *Number of species*

Group	Total at I.O.M. (1)	Southern species (2)	Northern species (3)	Widely distributed (4)	Confined to Great Britain (5)	Present at I.O.M. not Plymouth (6)	Present at Plymouth not I.O.M. (7)
Decapoda Reptantia	59	22	5	31	1	3	8
Decapoda Natantia	25	7	9	9	—	2	3
Mysidacea	22	7	9	6	—	3	3
Amphipoda	154	34	39	74	7	14	17
Isopoda	37	5	18	11	3	8	8
Cumacea	24	8	9	5	2	6	—
Total Crustacea	321	83	89	136	13	36	39
Echinodermata	39	6	7	26	—	2	4
Lamellibranchia	117	18	11	88	—	4	10
Gastropoda	114	27	15	72	—	5	12
Polychaeta	166	52	20	94	—	5	49
Total all groups	757	186	142	416	13	52	114

and Great West Bay (Holme, 1950) to the south, and the Danish and other Scandinavian waters to the north (Petersen, 1913, 1915; Blegvad, 1930; Molander 1928), and even the southern Icelandic waters (Einarsson, 1941). There is naturally a change in the composition of the fauna from north to south, but it is probable that the more successful animals have a wide geographical range because they are on the whole fairly tolerant of changes in temperature, and a list of the most abundant animals from any of the places mentioned above is very similar to those from the remainder. However, many of the less abundant species may be expected to have more limited ranges. Table 1 shows the result of a comparison between certain groups listed in Moore (1937), with later additions including those obtained during the present survey, and in the *Plymouth Marine Fauna* (Marine Biological Association, 1931).

Distribution is classified according to the best data available to me. Southern species are those that occur from Great Britain to the Mediterranean or farther south, northern species from Great Britain to Norway or farther north, and widely distributed species from the Mediterranean to Norway. Columns (1)–(5) include all species of the groups listed found at the Isle of Man or adjacent waters. Column (7) includes additional species recorded at Plymouth but not at the Isle of Man.

It will be seen that the majority, 55 %, of species found at the Isle of Man are of wide distribution. 1.5 % appear to be confined to the British Isles, but some may turn out to have a wider distribution. Of the remainder there is a slight preponderance of southern, 24.5 %, against northern forms, 19 %. Certain groups have a markedly southern distribution—Decapoda Reptantia and Polychaeta—whereas Isopoda seem to be mainly northern. It is to be

expected that more species would be found at Plymouth than in the Irish Sea, though the much greater number of Polychaeta found at Plymouth is probably due partly to more adequate collecting. The fauna of the Isle of Man is therefore mainly Atlantic-Boreal, with a slight excess of Mediterranean-Atlantic over Arctic-Boreal species. At Plymouth the Mediterranean-Atlantic influence is decidedly greater.

7. QUANTITATIVE RESULTS

Some results of an attempt to estimate the biomass on the various grounds is shown in Table 2

Table 2

Bottom-deposit	No. of samples	Mean weight animals (g. per m. ²)	Range in weight
Mud	13	34.8	4.9–112.8
Muddy sand (fine)	27	47.3	2.2–167.8
Muddy sand (coarse)	21	34.6	2.6–140.0
Fine sand	22	19.8	1.0–34.5

Each sample was obtained with the 0.1 m.² van Veen grab. Only the wet weight was estimated after removing surplus moisture with blotting-paper. The gut contents of large echinoids were removed before weighing, and large molluscs with thick and heavy shells, which were of rare occurrence, including *Cyprina islandica*, *Venus casina*, *Astarte sulcata*, and *Chlamy opercularis*, were omitted.

In the cases of muddy sand and mud the estimates are probably fairly accurate, since the grab obtained a good sample on each occasion, although the range in weight is large. On fine sand however, the grab scraped only the top few cm. of the deposit, probably

leaving certain animals untouched, and the mean weight may therefore be somewhat low.

Results of t tests for the sample weights of animals on pairs of grounds, using the formula

$$t = \bar{x} \sqrt{\frac{n_1 n_2 (n_1 + n_2 - 2)}{(n_1 + n_2) Sx^2}}$$

to test the hypothesis that the mean population weights are equal, are as follows:

Mud and fine muddy sand: $t = 1.03$, D.F. = 38, $P = > 0.3$.

Mud and coarse muddy sand: $t = 0.147$, D.F. = 32, $P = > 0.8$.

Mud and fine sand: $t = 2.197$, D.F. = 33, $P = < 0.05$.

Fine muddy sand and coarse muddy sand: $t = 1.06$, D.F. = 46, $P = 0.3 - 0.2$.

Fine muddy sand and fine sand: $t = 3.193$, D.F. = 47, $P = < 0.01$.

Coarse muddy sand and fine sand: $t = 1.54$, D.F. = 41, $P = 0.2 - 0.1$.

The sampled weight on fine sand is significantly lower than that on fine muddy sand and mud, using the 95 % probability level; and lower than that on coarse muddy sand, though statistically the difference is not significant. The fine sand ground carries a very low weight of animals per unit area, but the difference may be exaggerated by the imperfect action of the grab. It is possible that the mean weights on coarse and fine muddy sand are approximately equal, but a larger number of samples would be required to prove this, and any difference that may exist is likely to be small. Most of the biomass on the mud is due to the large echinoderm *Brissopsis lyrifera* and if this animal is ignored the greatest mass among the grounds investigated is probably found on muddy sand. However, although no figures can be quoted because the grab is entirely unreliable on these deposits, it is probable, judging from comparative dredge hauls, that a much greater mass per unit area is present on parts of the gravel and shell ground than on the muddy sand.

Comparison with other areas reveals that the fauna off the south of the Isle of Man is rather poor in weight of animals at the present time, though not in the number of species present. For example, fine muddy sand in an area off Whitehaven, Cumberland, carried in May 1950 a mean weight of animals of 243.8 g./m.² (40 samples), which is more than the highest value in any sample obtained off the Isle of Man, and more than five times the mean for the same type of deposit. The mean weight for fine sand was 45.5 g./m.² (30 samples), more than twice the mean found off the Isle of Man.

Blegvad (1930) gives tables showing the mean weight for various community areas in the Kattegat during the years 1919-26. The mean rough weights of living animals for hauls which were probably taken

on the grounds indicated are as follows: muddy sand, 218.0 g./m.²; fine sand, 61.2 g./m.².

These values are considerably higher than those on equivalent grounds off the Isle of Man, although in some years values as low as those on fine sand in Port Erin Bay were found on fine sand in certain parts of the Kattegat. It is on fine sand that the greatest fluctuations seem to occur, owing mainly to differences in the settlement of the larvae of lamellibranchs and worms, and it is possible that the mean weight per unit area for this ground is at its lowest ebb and will become greater. However, fine sand is too limited in extent to be important within the area dealt with in this paper, and for the remaining grounds there can be little doubt that the low mean weight is a permanent feature. A high biomass seems to be present in shallow estuarine waters or those with a considerable water renewal, while in deeper waters the biomass is lower (Spärck, 1935). The most probable factors causing this difference are the amounts of organic matter and nutrient salts discharged by rivers or brought in from deep water. The low biomass on muddy sand off the Isle of Man compared with those off the Cumberland coast or in the Kattegat is consistent with a low run off the land in the former place and a higher in the latter two. No evidence is available concerning differences in the amount of phosphate present.

An important aspect of quantitative investigations on the benthos is the possible relationship between the amount present in any area and the yield of the fisheries. It would be useful economically if it could be proved that there is normally a correlation between biomass and number of demersal fish. Unfortunately, while this may be so when large sea areas are compared one with another, it is not apparent in a detailed investigation. It is true that the low mean weight of bottom animals per unit area off the southern Isle of Man would indicate a rather poor fish population, and that the fishery, apart from that for pelagic fish, is not very productive, but it is not necessarily on the grounds with the highest benthos production that the most fish are caught. As an example, the Warts Bank, to the south of the Calf Sound, is composed of shell-gravel and contains very few animals that are taken in the bottom-sampler. The biomass is therefore very low when estimated with this instrument, but at certain times large numbers of cod and other fish are caught on the bank. In this case the fish are found to have been feeding on *Ammodytes* spp., which use the ground for shelter, but which are not obtained by the grab. Off the Cumberland coast the yield of plaice is much higher on fine sand than on muddy sand, while the reverse is true of the weight of invertebrates. Blegvad (1930) points out that those animals preferred as food by the plaice, which he terms first-class plaice food, are more important than the remainder;

if the weight of these alone is considered (in Blegvad's investigations fine sand 15.4 g./m.², and mudsands 15.8 g./m.²; off the Cumberland coast fine sand 12.3 g. and muddy sand 20.5 g.) the difference between the two grounds is much reduced. Nevertheless, plaice apparently show a preference for fine sand rather than for other grounds which is not directly related to the food supply, and it is probable that most species of fish tend to remain more on one type of ground than on others. The whole problem is further complicated by spawning and feeding migrations. It is possible that for any given species of fish there is a relation between the biomass present on similar grounds in different areas and the potential yield, but in the absence of comparable statistics of catches no conclusion can be reached.

8. SUMMARY

1. The bottom fauna within a radius of 15 miles from Port St Mary, Isle of Man, was surveyed during the period July 1946 to April 1950. Various sorts of

gear were used, including trawls, dredges and a 0.1 m.² van Veen bottom-sampler.

2. Four types of deposit were distinguished within the area: (a) coarse sands, gravels including shell, and stony ground, (b) fine sand, (c) muddy sand, (d) mud. Their limits are mainly fixed by wave action and the strength of the tidal currents.

3. The hydrographical conditions prevailing within the area are briefly described.

4. Each type of deposit carries a distinct faunal assemblage which may be considered as a main community. The fauna is not evenly distributed within each community area, but further subdivision was thought unjustifiable. An account is given of the communities and of the chief variations within them, with lists of the more important animals.

5. The fauna is compared from a zoogeographical viewpoint with that at Plymouth, and it is concluded that at the Isle of Man there is only a slight preponderance of southern against northern forms.

6. The biomass estimated from quantitative samples shows a poor production of benthos compared with that in some other areas.

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APPENDIX

Percentage occurrence of species for all hauls in which animals were identified. No figures are given for species occurring in less than 10 % of the hauls on any one ground (see p. 136).

Hauls have been allotted to grounds from records of the bottom deposits brought up as follows:

- A Coarse sands, gravels, shells and stones.
 A1 Fine gravels and calcareous algae. Hauls 1, 8, 13, 14, 36, 46, 49, 56, 59, 60, 62, 64, 65, 67, 82, 95, 96, 99, 147, 150, 184, 191 and 192.
 A2 Mixed coarse sand, gravels and shells, south and west of the Calf of Man. Hauls 5, 9, 15, 27-9, 50-3, 68, 70, 84, 89-91, 123, 181 and 183.
 A3 Gravels and stones, south of Port St Mary. Hauls 4, 26, 37, 39, 63, 85, 87, 88, 110, 166, 173-6 and 185.
 A4 Gravels, shells and stones, south and east of Langness. Hauls 92-4, 100, 101, 104, 106-9, 111, 112, 115, 117 and 188-90.
 A5 'Modiolus epifauna'. Hauls 7, 69, 86, 102, 103, 105, 114, 177, 186 and 187.
 B Fine sand. Hauls 47, 48, 58, 61, 66, 145, 152, 153 and 193-203.
 C Muddy sand.
 C1 Muddy sand with some gravel and broken shell. Hauls 2, 3, 10, 12, 16, 17, 20-25, 35, 40, 41, 54, 55, 57, 75, 76, 79-81, 97, 98, 113, 116, 118, 125, 127, 136-8 and 178.
 C2 Fine muddy sand. Hauls 6, 19, 34, 42, 43, 74, 78, 119, 121, 128-32, 139-43, 182, 204-14.
 D Mud. Hauls 11, 18, 30-3, 44, 45, 71-3, 77, 83, 120, 122, 133-5, 171, 172, 179, 180 and 215.

	Ground	...	...	A1	A2	A3	A4	A5	Total	B	C1	C2	Total	D
	No. of hauls	...	...	23	19	15	17	10	A	19	34	31	C	23
PORIFERA:														
<i>Desmacidon fruticosum</i> (Montagu)	—	—	—	—	5	—	—	60	8	—	—	—	—	—
COELENTERATA:														
<i>Tubularia indivisa</i> L.	—	—	—	—	—	20	12	10	7	—	—	—	—	—
<i>Abietinaria abietina</i> (L.)	4	15	13	18	30	14	—	—	14	—	6	—	3	—
<i>Hydrallmania falcata</i> (L.)	4	15	13	47	20	19	—	—	19	—	9	3	6	—
<i>Sertularia argentea</i> Ellis & Solander	—	11	7	18	50	13	—	—	13	—	3	—	1	—
<i>Nemertesia antennina</i> (L.)	—	26	7	12	10	11	—	—	11	—	12	3	8	—
<i>N. ramosa</i> (Lamouroux)	4	15	7	18	10	11	—	—	11	—	12	3	8	—
<i>Thecocarpos myriophyllum</i> (L.)	—	—	—	—	—	—	—	—	—	—	9	10	9	—
<i>Sarcodictyon catenata</i> Forbes	—	32	—	12	—	10	—	—	10	—	3	—	1	—
<i>Alcyonium digitatum</i> L.	—	5	13	18	20	10	—	—	10	—	—	—	—	—
<i>Tealia felina</i> (L.)	—	—	13	—	30	6	—	—	6	—	—	—	—	—
<i>Paracalythys taxilianus</i> Gosse	—	21	—	—	—	5	—	—	5	—	—	—	—	—
NEMERTINI														
<i>Tubulanus annulatus</i> (Montagu)	—	11	—	6	10	5	—	—	5	—	6	3	5	—
<i>Amphiporus pulcher</i> (Johnston)	—	5	—	12	30	7	—	—	7	—	3	—	1	—
Nemertine sp.	—	—	—	—	—	—	—	—	—	—	—	10	5	4
ARCHIANNELLIDA:														
<i>Polygordius lacteus</i> Schneider	13	—	—	—	—	4	—	—	4	—	—	—	—	—
POLYCHAETA:														
<i>Aphrodite aculeata</i> L.	—	—	7	12	—	4	—	—	4	—	—	10	5	—
<i>Hermione hystrix</i> (Savigny)	—	21	—	24	—	10	—	—	10	—	3	—	1	—
<i>Lepidonotus squamatus</i> (L.)	7	47	20	18	40	25	11	18	—	—	—	—	9	—
<i>Harmothoe haliaeti</i> McIntosh	7	26	7	—	—	10	—	—	10	—	6	—	3	—
<i>H. lunata</i> (Della Chiaje)	—	—	—	—	—	16	3	3	—	—	—	—	3	—
<i>Halosydna gelatinosa</i> (Sars)	—	32	7	18	10	13	—	—	13	—	—	—	—	—
<i>Sthenelais limicola</i> Ehlers	—	—	—	—	—	37	—	—	—	—	—	—	—	—
<i>Castalia punctata</i> (Müller)	—	15	—	—	10	5	—	—	5	—	9	—	5	—
<i>Oxydromus propinquus</i> Marion & Bobretzky	—	—	—	—	—	—	—	—	—	—	—	3	1	17
<i>Ophiodromus flexuosus</i> Della Chiaje	—	—	—	—	—	—	—	—	—	—	3	10	6	4
<i>Syllis spongicola</i> Grube	—	—	—	—	40	5	—	—	5	—	—	—	—	—
<i>S. armillaris</i> Malmgren	—	5	—	—	—	1	—	—	1	—	15	—	8	—
<i>Nereis pelagica</i> L.	—	—	13	—	40	7	—	—	7	—	—	—	—	—
<i>Nephtys incisa</i> Malmgren	—	—	—	—	—	—	—	—	—	—	41	81	60	74
<i>Nephtys</i> spp.	—	—	—	—	—	—	—	—	—	68	—	3	1	—
<i>Ephesia gracilis</i> Rathke	—	15	13	—	—	6	—	—	6	—	—	—	—	—
<i>Glycera convoluta</i> Keferstein	4	—	—	—	—	1	—	—	1	—	32	3	18	—
<i>G. lapidum</i> Quatrefages	43	5	—	—	—	13	—	—	13	—	—	—	—	—
<i>G. gigantea</i> Quatrefages	13	—	—	6	—	5	—	—	5	—	—	—	—	—
<i>G. rouxi</i> Audouin & Edwards	—	—	—	—	—	—	—	—	—	—	12	45	28	39
<i>Goniada maculata</i> Oersted	—	5	—	—	—	1	5	—	1	5	32	45	38	9
<i>Onuphis conchylega</i> Sars	—	—	—	—	—	—	—	—	—	—	12	3	8	—
<i>Lumbriconereis impatiens</i> Claparède	13	15	7	—	—	8	11	24	32	28	43	—	—	—
<i>L. fragilis</i> (Müller)	9	21	13	10	11	—	—	—	—	—	—	—	—	4
<i>Arabella iricolor</i> (Montagu)	—	—	—	—	—	—	—	—	—	—	12	10	11	—
<i>Prionospio cirrifera</i> Wiren	9	—	—	—	—	2	—	—	2	—	3	13	8	—
<i>Flabelligera affinis</i> Sars	—	26	—	—	—	6	5	—	6	5	—	—	—	—
<i>Diplocirrus glaucus</i> Haase	—	—	—	—	—	—	—	—	—	—	12	16	14	17
<i>Scalibregma inflatum</i> Rathke	4	—	—	—	—	1	—	—	1	—	27	16	22	13
<i>Ammotrypane aulogaster</i> Rathke	4	—	—	—	—	1	—	—	1	—	9	10	9	17
<i>Notomastus latericeus</i> Sars	4	—	—	—	—	1	—	—	1	—	18	65	40	65
<i>Owenia fusiformis</i> Della Chiaje	9	—	—	—	—	2	16	41	23	32	—	—	—	—
<i>Pectinaria auricoma</i> (Müller)	—	—	7	—	—	1	5	12	19	15	—	—	—	—
<i>P. koreni</i> Malmgren	—	—	—	—	—	—	11	3	—	—	—	—	—	—
<i>Amphicteis gunneri</i> (Sars)	—	—	—	—	—	—	—	—	—	—	24	23	23	—
<i>Polynnia nebulosa</i> (Montagu)	—	15	—	24	10	10	—	—	10	—	6	—	3	—
<i>Terebellides stroemi</i> Sars	4	5	7	—	—	4	—	—	4	—	21	13	17	—
<i>Pista cristata</i> (Müller)	17	—	—	—	—	5	—	—	5	—	21	—	11	—
<i>Serpula vermicularis</i> L.	—	47	7	—	40	17	—	—	17	—	9	3	6	—
<i>Hydroides norvegica</i> Gunnerus	4	37	—	12	10	13	—	—	13	—	3	3	3	—
<i>Pomatoceros triquetus</i> (L.)	9	47	20	35	50	30	—	—	30	—	6	—	3	—
<i>Filograna implexa</i> (Berkeley)	—	—	7	12	30	7	—	—	7	—	—	—	—	—
<i>Spirorbis spirillum</i> (L.)	4	11	7	—	30	8	—	—	8	—	6	—	3	—

Appendix (cont.)

	Ground No. of hauls	...	...	A1 23	A2 19	A3 15	A4 17	A5 10	Total A 84	B 19	C1 34	C2 31	Total C 65	D 23
GEPHYREA:														
<i>Phascolosoma vulgare</i> (Blainville)				4	37	7	—	—	11	—	3	3	3	—
<i>Phascolion strombi</i> (Montagu)				—	—	—	—	—	—	5	12	13	12	—
BRACHIOPODA:														
<i>Terebratula retusa</i> (L.)				—	47	—	—	—	11	—	3	—	1	—
<i>Crania anomala</i> (Müller)				—	42	—	—	—	10	—	—	—	—	—
CRUSTACEA:														
<i>Scalpellum scalpellum</i> (L.)				—	5	—	6	—	2	—	15	3	9	—
<i>Balanus porcatus</i> da Costa				9	32	7	12	50	19	—	12	—	6	—
<i>B. hameri</i> (Ascanius)				—	—	—	—	60	7	—	—	—	—	—
<i>Iphinoë serrata</i> (Norman)				—	—	—	—	—	—	—	18	13	15	4
<i>I. trispinosa</i> (Goodsir)				—	—	—	—	—	—	11	—	—	—	—
<i>Leucon nasica</i> (Kröyer)				—	—	—	—	—	—	—	—	—	—	26
<i>Eudorella emarginata</i> (Kröyer)				—	—	—	—	—	—	—	3	3	3	61
<i>Diastylis lucifera</i> (Kröyer)				—	—	—	—	—	—	5	3	13	8	4
<i>Conilera cylindracea</i> (Montagu)				13	11	7	—	—	7	—	6	—	3	—
<i>Eurydice inermis</i> Hansen				17	15	7	—	—	10	—	3	—	1	—
<i>Lysianassa plumosa</i> Boeck				4	15	—	—	—	5	—	12	—	6	—
<i>Perrierella audouiniana</i> (Bate)				—	5	—	—	40	6	—	—	3	1	—
<i>Scopelocheirus crenatus</i> Bate				—	5	7	—	—	2	—	15	6	11	4
<i>Ampelisca brevicornis</i> Costa				—	—	—	—	—	—	21	—	—	—	—
<i>A. spinipes</i> Boeck				4	5	—	—	—	4	—	38	19	29	—
<i>A. diadema</i> (Costa)				4	—	—	—	—	1	5	32	—	17	—
<i>A. typica</i> (Bate)				9	5	—	—	—	4	5	12	—	6	—
<i>A. tenuicornis</i> Lilljeborg				4	—	—	—	—	1	5	38	16	28	4
<i>Bathyporeia guilliamsoniana</i> (Bate)				—	—	—	—	—	—	21	6	—	3	—
<i>Urothoe elegans</i> Watkin				—	—	—	—	—	—	5	15	3	9	—
<i>Metaphoxus fultoni</i> (Scott)				13	15	—	—	—	7	—	6	—	3	—
<i>Harpinia pectinata</i> Sars				—	—	—	—	—	—	—	12	16	14	17
<i>H. crenulata</i> Boeck				—	—	—	—	—	—	—	6	10	8	30
<i>Leucothoe spinicarpa</i> (Abildgaard)				—	15	—	6	60	12	—	—	—	—	—
<i>Cressa dubia</i> (Bate)				—	15	7	—	10	6	—	18	3	11	—
<i>Lilljeborgia kinahani</i> (Bate)				9	21	7	—	—	8	—	—	—	—	—
<i>Nototropis veddomensis</i> (Bate & Westwood)				4	—	—	—	—	1	—	12	3	8	—
<i>Eusirus longipes</i> Boeck				4	21	7	—	—	7	—	6	3	5	13
<i>Cheirocratus intermedius</i> (Sars)				—	—	—	—	—	—	6	3	10	8	9
<i>Ceradocus semiserratus</i> (Bate)				9	26	—	—	—	8	—	—	—	—	—
<i>Maera othonis</i> (Milne Edwards)				13	11	7	—	—	7	5	27	3	15	—
<i>Lembos longipes</i> (Lilljeborg)				—	5	—	—	—	1	—	15	10	12	—
<i>Eurystheus erythrophthalmus</i> (Lilljeborg)				9	32	13	—	10	13	—	9	3	6	—
<i>Phisica marina</i> Slabber				4	11	—	—	—	4	5	15	3	9	—
<i>Erythrops serrata</i> (Sars)				—	—	—	—	—	—	—	—	—	—	13
<i>Pseudomma affine</i> Sars				—	—	—	—	—	—	—	3	—	1	13
<i>Pandalus montagui</i> Leach				9	37	7	18	50	21	—	12	3	8	13
<i>P. bonnier</i> Caullery				—	—	—	—	—	—	—	3	—	1	13
<i>Pandalina brevivirostris</i> (Rathke)				4	11	—	24	20	11	—	3	3	3	—
<i>Spirontocaris pusilla</i> (Kröyer)				—	32	7	18	20	14	—	—	—	—	—
<i>Alpheus ruber</i> Milne Edwards				—	—	—	—	—	—	—	6	13	9	9
<i>Processa canaliculata</i> Leach				—	—	—	—	—	—	—	—	3	1	13
<i>Cragon allmanni</i> Kinahan				—	5	—	—	—	1	—	3	—	1	13
<i>Philocheras echinulatus</i> (Sars)				—	—	—	—	—	—	—	6	—	3	17
<i>Nephrops norvegicus</i> L.				—	—	—	—	—	—	—	3	—	1	22
<i>Calocaris macandreae</i> Bell				—	—	—	—	—	—	—	—	—	—	70
<i>Galathea intermedia</i> Lilljeborg				22	42	13	47	40	32	—	27	—	14	—
<i>G. dispersa</i> Bate				—	32	7	6	10	11	—	15	6	11	—
<i>G. nexa</i> Embleton				—	15	7	—	40	10	—	—	—	—	—
<i>Porcellana longicornis</i> (L.)				4	32	20	18	50	21	—	9	6	8	—
<i>Eupagurus bernhardus</i> (L.)				9	26	27	41	40	26	—	9	3	6	—
<i>E. prideauxi</i> (Leach)				—	32	13	53	10	21	—	18	10	14	—
<i>E. cuanensis</i> (Thompson)				—	15	—	41	10	13	—	—	—	—	—
<i>E. pubescens</i> (Kröyer)				—	32	20	24	40	20	—	3	—	1	—
<i>Anapagurus laevis</i> (Thompson)				—	—	—	6	—	1	—	9	19	14	—
<i>A. chiroacanthus</i> (Lilljeborg)				13	21	—	12	—	11	—	12	—	6	—
<i>Portunus pusillus</i> Leach				17	32	7	35	—	20	—	12	—	6	—
<i>P. depurator</i> (L.)				4	21	—	6	—	7	—	9	3	6	—
<i>Xantho couchi</i> Bell				—	26	—	—	40	11	—	3	—	1	—
<i>Pinnotheres pisum</i> (Pennant)				—	15	—	12	30	10	—	—	—	—	—
<i>Ebalia tuberosa</i> (Pennant)				13	53	13	47	30	31	—	24	—	12	—
<i>Eurynome aspera</i> (Pennant)				4	15	—	6	30	10	—	12	3	8	—
<i>Pisa gibbsi</i> (Leach)				—	11	—	18	30	10	—	—	—	—	—
<i>Hyas coarctatus</i> Leach				—	58	33	41	80	37	—	12	3	8	—
<i>Inachus dorsettensis</i> (Pennant)				4	26	—	29	30	17	—	12	3	8	—
<i>Macropodia longirostris</i> (Fabricius)				—	32	7	12	40	16	—	12	3	8	—
<i>M. rostrata</i> (L.)				4	15	7	12	20	11	—	3	—	1	—
MOLLUSCA:														
<i>Lepidopleurus asellus</i> (Gmelin)				22	47	7	18	—	21	—	9	—	5	—
<i>Nucula sulcata</i> Bronn				—	—	—	—	—	—	—	3	19	11	26
<i>N. hanleyi</i> Winckworth				43	11	—	—	—	14	—	6	—	3	—
<i>Glycimeris glycimeris</i> (L.)				43	63	60	65	40	54	—	3	—	1	—
<i>Monia squama</i> (Gmelin)				—	47	—	12	50	19	—	6	—	3	—
<i>Modiolus modiolus</i> (L.)				9	53	47	77	100	50	—	—	—	—	—
<i>Pecten maximus</i> (L.)				17	37	7	18	—	18	—	18	—	9	—
<i>Chlamys varia</i> (L.)				—	15	—	—	50	10	—	—	—	—	—
<i>C. distorta</i> (da Costa)				—	5	—	—	50	7	—	3	—	1	—

Appendix (cont.)

	Ground No. of hauls	...	...	A1 23	A2 19	A3 15	A4 17	A5 10	Total A 84	B 19	C1 34	C2 31	Total C 65	D 23
MOLLUSCA (cont.):														
<i>C. opercularis</i> (L.)	—	—	—	4	63	13	71	40	37	—	41	13	26	—
<i>C. tigrina</i> (Müller)	—	—	—	—	42	20	24	20	20	—	12	—	6	—
<i>C. striata</i> (Müller)	—	—	—	9	32	13	—	10	13	—	15	3	9	—
<i>Lima loscombi</i> Sowerby	—	—	—	4	42	33	41	30	29	—	12	—	6	—
<i>L. subauriculata</i> (Montagu)	—	—	—	—	—	—	—	—	—	—	6	16	11	—
<i>Astarte sulcata</i> (da Costa)	—	—	—	—	42	40	6	10	19	—	18	—	9	—
<i>Montacuta substriata</i> (Montagu)	—	—	—	—	11	7	18	10	8	—	—	—	—	—
<i>M. ferruginosa</i> (Montagu)	—	—	—	—	—	—	—	—	—	16	—	10	5	4
<i>Cardium scabrum</i> Philippi	—	—	—	9	5	—	—	—	4	—	12	6	9	—
<i>Dosinia lupinus</i> (Montagu)	—	—	—	—	—	—	—	—	—	21	18	10	14	—
<i>Venus casina</i> L.	—	—	—	13	21	47	24	40	26	—	12	3	8	—
<i>Venus ovata</i> Pennant	—	—	—	17	21	7	6	—	12	—	24	3	14	—
<i>V. fasciata</i> (da Costa)	—	—	—	30	47	13	41	—	30	—	6	—	3	—
<i>V. striatula</i> (da Costa)	—	—	—	—	—	—	—	—	—	74	—	3	1	—
<i>Paphia rhomboides</i> (Pennant)	—	—	—	17	15	13	12	—	13	—	6	—	3	—
<i>Mysia undata</i> (Pennant)	—	—	—	—	—	—	—	—	—	—	—	16	8	—
<i>Tellina fabula</i> Gmelin	—	—	—	—	—	—	—	—	—	79	—	—	—	—
<i>Abra prismatica</i> (Montagu)	—	—	—	—	—	7	—	—	1	21	32	61	46	26
<i>Gari fervensis</i> (Gmelin)	—	—	—	—	—	—	—	—	—	16	3	—	1	—
<i>G. tellinella</i> (Lamarck)	—	—	—	48	11	20	24	—	24	—	—	—	—	—
<i>Cultellus pelucidus</i> (Pennant)	—	—	—	—	5	—	—	—	1	11	21	29	25	—
<i>Ensis ensis</i> (L.)	—	—	—	9	—	—	6	—	4	11	—	—	—	—
<i>Spisula elliptica</i> (Brown)	—	—	—	30	11	—	12	—	13	—	12	6	9	—
<i>Aloidis gibba</i> (Oliv)	—	—	—	—	—	—	—	—	—	—	29	29	29	4
<i>Hiatella arctica</i> (L.)	—	—	—	—	26	7	—	20	10	—	6	—	3	—
<i>Thracia phaseolina</i> (Lamarck)	—	—	—	—	—	—	—	—	—	5	3	13	8	—
<i>T. villosuscula</i> (MacGillivray)	—	—	—	17	5	—	—	—	6	—	—	—	—	—
<i>Dentalium entalis</i> L.	—	—	—	4	5	—	—	—	2	—	44	3	25	—
<i>Emarginula reticulata</i> Forbes & Hanley	—	—	—	—	47	7	24	20	19	—	3	—	1	—
<i>Diodora apertura</i> (Montagu)	—	—	—	—	21	—	12	—	7	—	—	—	—	—
<i>Calliostoma xizyphium</i> (Lamarck)	—	—	—	4	32	13	29	80	26	—	3	3	3	—
<i>C. papillosum</i> (da Costa)	—	—	—	—	5	7	12	—	5	—	6	3	5	—
<i>Gibbula magus</i> (da Costa)	—	—	—	17	—	—	—	—	5	—	—	—	—	—
<i>G. tumida</i> (Montagu)	—	—	—	30	21	13	6	—	17	—	3	—	1	—
<i>Turritella communis</i> Risso	—	—	—	—	—	—	—	—	—	—	18	48	32	—
<i>Eulima trifasciata</i> (Adams)	—	—	—	9	11	—	6	—	6	—	6	—	3	—
<i>Capulus ungaricus</i> (L.)	—	—	—	—	11	—	6	40	8	—	—	3	1	—
<i>Aporrhais pes-pelican</i> da Costa	—	—	—	—	—	—	—	—	—	—	15	3	9	—
<i>Natica poliana</i> Forbes	—	—	—	22	21	—	6	10	13	16	15	3	9	—
<i>Velutina velutina</i> (Müller)	—	—	—	—	15	—	6	—	5	—	6	—	3	—
<i>Colus gracilis</i> (da Costa)	—	—	—	—	11	—	18	20	8	—	—	—	—	—
<i>Buccinum undatum</i> L.	—	—	—	—	26	13	53	80	29	—	—	—	—	—
<i>Tricla lignaria</i> Leach	—	—	—	4	11	—	—	—	4	—	9	—	5	—
<i>Sepiolo atlantica</i> Orbigny	—	—	—	—	5	7	6	10	5	—	3	3	3	9
POLYZOA:														
<i>Flustra foliacea</i> (L.)	—	—	—	—	5	13	41	10	13	—	3	—	1	—
<i>Cellaria fistulosa</i> (L.)	—	—	—	9	15	13	—	—	8	5	18	3	11	—
ECHINODERMATA:														
<i>Antedon bifida</i> (Pennant)	—	—	—	4	5	13	18	10	10	—	9	—	5	—
<i>Luigia ciliaris</i> (Philippi)	—	—	—	—	21	7	—	—	6	—	3	—	1	—
<i>Porania pulvillus</i> (Müller)	—	—	—	4	47	7	—	—	13	—	12	6	9	—
<i>Palmipes membranaceus</i> Linck	—	—	—	4	15	—	—	—	5	—	9	3	6	—
<i>Solaster papposus</i> (L.)	—	—	—	9	47	27	47	40	32	—	15	—	8	—
<i>Henricia sanguinolenta</i> (Müller)	—	—	—	—	42	7	65	40	29	—	—	—	—	—
<i>Asterias rubens</i> L.	—	—	—	22	42	27	29	80	36	—	18	6	12	—
<i>Ophiothrix fragilis</i> (Abildgaard)	—	—	—	9	32	100	53	90	49	11	6	3	5	—
<i>Ophicomina nigra</i> (Abildgaard)	—	—	—	26	32	33	47	40	36	5	15	—	8	—
<i>Ophiopholis aculeata</i> (L.)	—	—	—	4	37	20	—	50	19	—	9	3	6	—
<i>Amphiura filiformis</i> (Müller)	—	—	—	4	—	7	—	—	2	16	38	32	35	—
<i>A. securigera</i> (Düben & Koren)	—	—	—	13	11	—	—	—	6	—	—	—	—	—
<i>Ophiura texturata</i> Lamarck	—	—	—	—	—	—	6	—	1	5	12	6	9	—
<i>O. albida</i> Forbes	—	—	—	48	—	7	41	—	23	16	47	10	29	—
<i>Psammehinus miliaris</i> (Gmelin)	—	—	—	35	53	53	47	80	50	—	24	6	15	—
<i>Echinus esculentus</i> L.	—	—	—	17	37	33	71	90	45	—	9	—	5	—
<i>Echinocyamus pusillus</i> (Müller)	—	—	—	48	47	27	12	—	31	11	24	6	15	—
<i>Spatangus purpureus</i> Müller	—	—	—	22	32	27	82	50	40	—	—	—	—	—
<i>Echinocardium cordatum</i> (Pennant)	—	—	—	—	—	—	—	—	—	26	—	—	—	—
<i>E. flavescens</i> (Müller)	—	—	—	4	21	27	—	—	11	—	47	10	29	—
<i>Brissopsis lyrifera</i> (Forbes)	—	—	—	—	—	—	—	—	—	—	18	45	31	43
<i>Cucumaria lactea</i> (Forbes)	—	—	—	9	15	—	—	—	6	—	3	—	1	—
<i>Thyone fusus</i> (Müller)	—	—	—	4	5	—	—	—	2	—	12	—	6	—
<i>Leptosynapta inhaerens</i> (Müller)	—	—	—	9	—	—	—	—	2	5	18	6	12	—
TUNICATA:														
<i>Molgula occulta</i> Kupffer	—	—	—	—	—	—	—	—	—	5	18	—	9	—
<i>Ascidia mentula</i> (Müller)	—	—	—	—	5	7	6	40	8	—	6	—	3	—
PISCES:														
<i>Callionymus lyra</i> L.	—	—	—	9	—	—	12	—	5	—	3	6	5	—
<i>Lepadogaster bimaculatus</i> (Donovan)	—	—	—	4	21	—	12	30	12	—	—	—	—	—
<i>Gobius jeffreysii</i> Günther	—	—	—	—	11	—	6	—	4	—	3	—	1	—
<i>Lebetus scorpioides</i> (Collett)	—	—	—	—	32	—	12	10	11	—	—	—	—	—
<i>L. orca</i> (Collett)	—	—	—	—	15	—	—	—	4	—	—	—	—	—

REVIEWS

THE HISTORY OF THE DISTRIBUTION
OF THE EUROPEAN FRESH-WATER FAUNA

A. Thienemann (1950). *Verbreitungsgeschichte der Süßwassertierwelt Europas*. Die Binnengewässer, 18: i-xvi and 1-809, 249 text-figs. E. Schweizerbart, Stuttgart.

The history is traced from the end of the Tertiary epoch to the present day, a period of which the main event was the Ice Age.

About what befell the fauna during the changes that this caused, there is little direct evidence, and the story of the past history of any species must be pieced together chiefly from its distribution to-day. A certain caution must, therefore, be exercised in drawing conclusions, a caution that is not invariably found in writings on geographical distribution; it is scarcely necessary to say that Prof. Thienemann, Director of the German Freshwater Biological Station at Plön for many years, makes no glib assumptions, but examines each theory and possible alternatives and objections to it with scholarly impartiality.

Much of the evidence depends on the relation between the range of a species and certain barriers to spread through fresh water that arose at different periods, and therefore can be based only on such groups as fish, Crustacea, planarians, and water-mites—that is, rather a limited portion of the fresh-water fauna. Insects, which are usually able to fly at some stage in their lives, can traverse these barriers and therefore their distribution reveals little about past history, unless the barrier is a physiological one, such as inability to withstand high or low temperature, when they are as valuable as any other group for the present study. That conclusions cannot be based on distribution unless the ecological requirements of a species are known is also made clear.

Briefly the history of the fresh-water fauna of Europe is as follows. The climate at the end of the Pliocene was much as it is to-day. The fauna too was similar, but richer. Then came the Ice Age, and, for middle Europe, climatic conditions similar to those of tundra regions to-day. Cold-loving Arctic and alpine species advanced with the ice, and many of them joined up in the middle with each other and with hardy species that had lived there in temperate times. The rest of the temperate fauna was driven south, some of it right down into the 'refuge areas' of Iberia, Italy, the Balkans, and the Caspian region; many species probably perished.

Then the ice began to retreat; there were in fact several advances and retreats, but in general it is not possible to separate the effects on the fauna of individual glacial and interglacial periods. The cold-water animals retreated too, some still confined to the Arctic or alpine fringe, but many now established in both cold zones; some stayed behind in locally favourable places such as springs. Other animals that flourish in cold conditions but are not restricted to them by physiological requirements withdrew, as the temperate fauna came back, to moorland localities, in the difficult conditions of which competition was less intense.

Many of the refugees in southern Europe have remained there ever since, but others returned to mid-Europe as the ice retreated in late glacial and early postglacial times. Some, for reasons which are obscure, did not start until later, and a few are extending their range even now. To Thienemann the study of geographical distribution is not the study of something fixed and immutable, as it is to some authors.

The volume is divided into six main chapters, each almost a book in itself. The first is an essay on ecology, the next three describe the fauna of preglacial, glacial, and early postglacial times respectively. Chapter E describes later changes in the fauna, and chapter F is devoted to immigrants that have come in during the last century or so, that is during the time when man with his ships and canals has been an important factor in the distribution of animals. Though nothing could appear more straightforward than this treatment, the reader should be warned that the Ice Age itself is not described till chapter C, though the argument in chapter B involves a fair knowledge of the subject.

Chapter A (166 pp.) opens with a delightful essay showing how the distribution of *Mysis relicta* is determined by past events and present-day requirements. Let not the reader delude himself that other stories are as clear and simple. The 'ecological valency', that is the range of variation in environmental factors that a species can tolerate, is then discussed. Many terms are defined, for example: euryök, eurytop, euryvalent, euryplastisch and the corresponding opposites, stenök, etc. It is pertinent to remark that most of these terms do not appear again in the book. It is concluded that, though there are notable exceptions, the ecological valency of any one species tends to remain constant. The next subjects are first, optimal conditions and the composition of communities, and secondly, factors that determine the occurrence of organisms. Under the latter head are discussed: the time factor, remoteness, and chance; heat, light, water movements, calcium, sodium chloride, humus, pollution, oxygen, and other chemical factors; food, and other relationships between animals; and means of dispersal. During the chapter Thienemann expresses disagreement with the idea that every ecological niche is filled.

Chapter B (133 pp.) starts with an account of archaic forms such as the Dipnoi, various Amphibia, Crustacea such as *Bathynella* and *Anaspides*, and a planarian. These were once much commoner, and have failed to withstand the competition of more modern forms. Some probably disappeared from Europe when the ice came, and it is noteworthy that most of those surviving to-day occur in subterranean waters (*Proteus*, *Bathynella*, *Parabathynella*), an environment that has provided a refuge because there is little competition in it.

The chapter's second subheading is 'Preglacial elements in the European fresh-water fauna', and it starts with some remarks on the fossil record. This is found to be fragmentary; fossiliferous deposits have been found in only a few places and they contain only those animals that have hard parts to preserve. Most of the fossils found in

the late Pliocene belong to species known to-day. When the distribution of the present-day fauna is surveyed, and changes brought about by the Ice Age considered, the conclusion is that all the species, except a few modern immigrants, occurring in Europe now were there before the Ice Age. The rest of the chapter is devoted to animals with a restricted distribution. They are placed in three categories, the first of which includes the snail *Melanopsis*, confined to warm springs and believed to be a relict from the time when Europe had a subtropical climate. In the second comes the subterranean fauna, made up in part from marine immigrants that possibly entered fresh water in an earlier epoch when the climate was warmer and in part from ancient fresh-water animals. It includes representatives of the Archannelida and the Polychaeta. Most of this fauna occurs in the Balkans, where there are extensive underground caves and channels in the limestone. It is sparse farther north, perhaps because the Ice Age wiped it out and it has never got back. The third comprises those animals which, driven south by the ice, have never returned from the refuge areas. Fifteen pages are devoted to the remarkable fauna of Lake Ohrid [Ochrida] in south-west Yugoslavia, a lake which later, in the summary, Thienemann describes as a museum of living Tertiary fossils. Of the fauna that has remained in the other refuge areas, Iberia, Italy and the Caspian region, only the fish are sufficiently well known to illustrate the principle.

Chapter C (125 pp.) starts with an account of the Ice Age. This is a short account covering only ten pages, on which there are five diagrams. It is based on the book by Woldstedt and does not attempt to discuss the controversies that rage round the interpretation of the glacial record, which presents such difficulties as apparently four main glaciations in the Alps, but only three in northern Europe. The reader is somewhat puzzled at first to find subheadings showing three glacial (p. 305) and three interglacial periods (pp. 309-12). Lists of fossils found in the interglacial periods are given, but they do not help greatly with the interpretation of faunistic changes. The last interglacial period is the only one in which conclusions about the distribution of particular species can be made. The final glaciation did not extend as far south as the preceding one and did not cover the west coast of Denmark. The grayling and the mussel, *Margaritifera*, occur only in those Danish rivers that flow to the North Sea, and from this it is deduced that they occurred in Denmark in the last interglacial period. There follows an account of the discontinuous distribution of certain species which occur in the Holarctic and the Palaearctic, and in east and west but not mid-Eurasia, and of species which are distinct in one of these areas but obviously closely related to a species in the other. The separation of the Eurasian and American land-masses took place in the Tertiary period; the separation of the Palaearctic fauna into eastern and western groups was brought about by the Ice Age, glaciation reaching its most southerly point near the Black Sea, the shores of which it nearly touched. The last ninety pages of the chapter are devoted to the fauna of the northern and alpine glacier margins and to that of the mixed fauna between them.

Chapter D (166 pages) opens with general remarks on changes in fresh-water habitats likely as the ice retreated.

The amount of water grew less as the glaciers reached a point of stability, and extensive pool-formation on frozen ground as snow melted—a phenomenon well known in the north to-day—disappeared. Lakes became thermally stratified and began slowly to change from an oligotrophic to a eutrophic condition, some evolving more rapidly than others, so that it is possible to deduce past changes by studying lakes at different stages of development to-day.

The most important part of the chapter is about events that took place in the Baltic region. As the ice receded over the north German coast, it left a great fresh-water lake behind it. When the ice reached the lowlands of south Sweden, then below sea-level, sea water flowed in and formed the *Yoldia* sea. This was cut off when southern Sweden rose as the load of ice on it grew lighter, and the fresh-water *Ancylus* lake (7500-5500 B.C.) was formed. Then a subsidence joined the *Ancylus* lake and the sea, between Denmark and Sweden where the channel runs to-day, and the *Littorina* sea came into being. The same subsidence severed England from the continent. Certain marine animals trapped in the *Yoldia* sea or in the sea that existed in the area during the last interglacial period, survived the change to fresh water and exist to-day in lakes that were left isolated when the level of the *Ancylus* lake fell.

To conclude the chapter, Thienemann returns to the Arctic, alpine, Arctic-alpine, and relict faunas giving species lists and discussing explanations of their origins alternative to the one put forward in the previous chapter. Most of the species separated since the Ice Age are still homogeneous; some have split into recognizable races and a few have reached a stage where taxonomists list two distinct species.

Chapter E (64 pages) describes with the aid of numerous maps the distribution of certain fishes that have clearly re-invaded north Europe since the Ice Age, usually since the subsidence that isolated Britain, for absence from Britain is one of the important pieces of evidence in many of the stories. Other groups are, of necessity, dealt with more summarily. There is an interesting group of Trichoptera that occurs in south and south-west Europe and also along the Rhine and its tributaries, from which it is deduced that the group has spread up the Rhone from the south, flown in the adult stage over the watershed, and continued down the Rhine Valley. Certain warmth-loving species are absent from places where they might be expected. Thus *Planaria gonocephala* is absent from the Baltic Island of Rügen, though the conditions of the lower parts of streams there appear to be suitable for it. Rügen was joined to the mainland at the time when the postglacial climate was at its warmest and, as *P. gonocephala* occurs on the mainland, it almost certainly reached the island too. Rügen was cut off when the *Littorina* sea was formed and after that the climate deteriorated. The streams probably reached a temperature at which *Planaria gonocephala* could not keep a foothold in competition with *Polycelis cornuta*. When the climate ameliorated, the way back was barred by the sea.

Evidence is produced that warm periods in recent times (e.g. 1856-65) have resulted in an unusual abundance in Germany of certain Mediterranean species.

Chapter F (60 pages) lists and describes the history and biology of twenty-six newcomers to Germany during the

recent period when man has been traversing the world in ships and assisting the spread of introduced aliens at home by cutting canals. The muskrat, six fishes, and the American crayfish, *Cambarus affinis*, have been introduced deliberately. Two species have been introduced by aquarium lovers. Eleven have come on or in ships. Some of these, such as the zebra mussel and the mitten crab, have spread with astonishing speed, others are still confined to the point of introduction. Five species, *Echinogammarus berilloni* and *Asellus meridianus* for example, have invaded Germany from other parts of Europe.

This is a long book. Prof. Thienemann writes in an expansive style associated with an earlier epoch in this paper-restricted country. He writes as one who enjoys expounding, starting each fresh topic with a neat well-rounded introduction and finishing in the same way. In the middle he has no hesitation in saying the same thing in two different ways if he wishes to emphasize a point. It makes the book pleasant and easy to read. Nor, I think, is the amount of repetition to be cavilled at in a book of this size. On the other hand, the frequent and extensive quotations from other authors do not all seem necessary. The book presents with full data and plenty of discussion an amazing mass of information; it is not possible in a review of this length even to mention every subject, many little-known and fascinating, discussed—the chapter headings and subheadings occupy six pages. Nor is it merely a treasure-house of isolated facts; the whole is skilfully written about a central theme.

The Ice Age and its effect on the fauna has interested continental fresh-water biologists for many years, and Thienemann has now collated all their work. Nobody will agree with everything that he has written, nor will all the theories survive further investigation; the author himself would be the last to expect either of these two things. He has summed up the situation as it stands to-day and his summing-up provides a springboard for further work. To anybody concerned with the geographical distribution of fresh-water animals the book will be indispensable; few other faunistic workers will not profit by having it available for reference. It has nothing for the physiologist, except one who is looking for a problem to tackle. Outside the sphere of fresh-water biology its interest will be limited, though students of terrestrial groups may find some of the geological data and the references thereto useful.

There are 249 black-and-white illustrations, a number of them maps. Taken from many different sources, they vary considerably in quality, and more care could have been taken over correlating the text with some of them. Thus the names used on p. 433 are not those shown on Fig. 146 and recourse must be had to an atlas before the paragraph is intelligible. Cross-references both to statements in the text and to figures could have been used with advantage. For example I first noted on p. 355 the lack of a map showing drainage during the Ice Age, but did not discover that there was such a map till I reached p. 591. Fig. 103, on p. 301, shows the limit of the last glaciation, but shows it only on the continent, and there is nothing to tell the interested reader that there is a map devoted entirely to the British Isles and to the limits of glaciation on p. 467. (Incidentally, though, as noted, the fauna of England and Scotland is of

critical importance, little is said about the fauna of Ireland.) The numbering of the key to Fig. 207 is upside down, and 1 should be at the top where it would be expected. In line 10 of p. 390 'späteren' should surely read 'früheren'.

There are 45 pages of references, and the number of works referred to must be about 1000. The index is divided into a 7-page index of things and a 20-page index of names. There is an excellent 20-page summary with extensive page references and this, together with the full contents list already mentioned, greatly enhances the value of a book that few in Britain are likely to read from cover to cover. The print is large, the paper of good quality; but the backing is paper, and the review copy is not bound completely, many of the sheaves of pages being loose.

T. T. MACAN

CLOACA MAGNA AVIUM: THE SPECIALIST ON GUANO

G. E. Hutchinson (1950). *Survey of contemporary knowledge of biogeochemistry. 3. The biogeochemistry of vertebrate excretion.* Bull. Amer. Mus. Nat. Hist. 96: 554 pp., 16 plates, and 56 tables. Price \$ 10.00.

The purpose of the 'Survey of contemporary knowledge of biogeochemistry' is to 'bring together and publish as a series of monographs the available information on all aspects of the interrelations of biology and geochemistry', and Prof. Hutchinson's monograph provides the third in this series. In spite of its profound title this is a study of aspects of the production, deposition and chemistry of 'guano', and although eighty pages are devoted to guano formed by cave-dwelling bats the primary emphasis is on guano produced by sea-birds.

The material is organized by geographical units with each unit examined in terms of oceanography, climatology, ornithology and chemistry, and where sufficient data exist the total quantity of guano is estimated. In some guano areas, notably the islands off the western coasts of Peru and Chile, numerous scientists have conducted research of fundamental importance so that there exists in the literature sufficient material for detailed treatment. The section of the monograph which discusses this is of considerable ecological interest.

Three species of guanay bird produce virtually all the guano found in the modern deposits of the Peruvian islands, and Vogt has done a comprehensive study of their ecology. Feeding primarily on the anchoveta (*Engralis ringens*), these guanay move from island to island in response to their food supply, exhibiting complex feeding and nesting behaviour patterns. The first male birds to become sexually active choose the best nesting territories from which the colonies grow peripherally, and birds just entering the breeding cycle on other islands are drawn to these established colonies. Although the habit of aggregation does not produce synchrony of breeding, the size of the colony is of biological value in that the larger the colony the fewer the nests exposed to the peripheral danger zone. Vogt has estimated 10,000 birds as the minimum number of the cormorant *Phalacrocorax bougainvillei* necessary to the establishment of a successful breeding colony. Although the nests which are at a mean

density of 3.139 ± 0.038 per m.² are defended as territories, the islands themselves have apparently no meaning as such, and are deserted in periods of food scarcity.

During these wholesale desertions which occur periodically, the adult birds leave their eggs and chicks, and often die in large numbers at sea or find their way to the mainland where they may die before being able to return to the islands. Lavalle has introduced evidence correlating these catastrophes with abnormal extensions southwards and seawards of warm water, and subsequent catastrophes have tended to confirm his conclusions. The incursions are accompanied by periods of abnormal rainfall conforming to a traditional 7-year periodicity.

Vogt calculates that one adult guanay bird produces 15.8 kg. of guano per year, and using this figure Prof. Hutchinson has constructed a population curve based upon the annual yield of guano on the Peruvian islands from 1909 to 1943. Although approximate, this curve seems to correspond with other information on these population fluctuations. The Compañía Administradora del Guano has kept a series of records noting the presence or absence of *Engralis* shoals as observed by company guardians stationed on the islands, and in spite of geographical variation these records show a definite pattern of abundance and scarcity.

Two hypotheses have been proposed to explain the variations in food supply. Vogt treats the minima as real *Engralis* deficiencies due to migration, while Schweigger treats the scarcities as apparent, and states that during warm water incursions the anchoveta remain with their planktonic food supply beneath the thermocline which develops during the daytime, and are therefore unavailable as a food source to the diurnal guanay birds. Evidence supporting the latter thesis is inconclusive, and further work remains to be done on the problem.

The chronology of the Peruvian deposits has been a popular area of study and conjecture since the work of Von Humboldt. As the orography of the Peruvian coast is Tertiary and since the guano birds appear to be taxonomically ancient, most workers have reasoned *a priori* that the deposits are of the remote past. Murphy treated the problem as insoluble, and considered the guano caps to be in a steady state in which collective erosion factors equalled the rate of deposition. Applying a 'climatological interpretation' to the available data, Prof. Hutchinson concludes that before 2000–3000 years ago the Peruvian coast was unsuitable to the formation of guano. Although the present 7-year rainfall cycle is real it is not believed to be of antiquity, and it is likely that until 2000–3000 years ago there were phases of heavy rainfall which prevented guano deposits from being formed.

Considerable attention is given to the chemistry of guano, and several important conclusions emerge from these discussions. The biological data are used to evaluate the quantitative role of sea-birds in the general geochemical cycles of the elements present in guano. Phosphorus is the element appearing in greatest concentration, and as sea-birds remove annually from sea to land only a small fraction of the phosphorus entering the sea through chemical erosion, their role in the general phosphorus cycle is judged as negligible. This is taken to preclude their importance in the general geochemical cycles of other elements.

This work succeeds in compiling a vast number of facts documented by over 950 references, and it contains valuable information for ecologists. The stated purpose of the survey to correlate 'available information on all aspects of the interrelations of biology and geochemistry' is, however, exceedingly ambitious, and although Prof. Hutchinson has performed a feat of scholarly research, the resulting chaos of fact makes this a cumbersome monograph for practical use.

RICHARD S. MILLER

SOME RECENT AUSTRIAN STUDIES ON TERRESTRIAL ECOLOGY

Almost simultaneously, Dr Herbert Franz of Admont and Prof. Wilhelm Kühnelt of Vienna have published books on soil zoology.

In the prefaces they express their thanks to a considerable number of Austrian ecologists who are little known outside Austria. This is a list picked at random: Donner, Gretschy, Jahn, Leitner, Paesler, Riha, Schaller and Wittasek. They are only examples, but how many countries can conjure up even this number of terrestrial animal ecologists? These younger ecologists have produced a considerable part of the primary material used in the two books. Prof. Kühnelt's book, especially, is valuable because it introduces several of them to the reader. One important Austrian work, from the Zoologisches Institut, University of Innsbruck, is not mentioned in either of the two books, and it certainly deserves the attention of terrestrial ecologists:

Heinz Janetschek (1949). *Tierische Successionen auf hochalpinem Neuland. Nach Untersuchungen am Hintereis-, Niederjoch- und Gepatschferner in den Oetztaler Alpen.* Ber. Naturw.-Med. Ver. Innsbruck. 48-9: 1-215, 18 text-figs. and 7 plates. Universitätsverlag, Innsbruck.

The Hintereis glacier is classical ground in glaciology. Blumcke and Hess studied this locality in the eighteen-nineties and several others have contributed to the glaciology of the area. The retrogression of the glacier is about 30 m. per year, with sudden forward pushes in 1850, c. 1860, 1890 and 1920. The front of the glacier in these years has left end moraines which divide the foreland of the glacier into four zones that have been ice-free for 80, c. 65, 45 and 15 years respectively. During the nineteen-thirties Friedel studied the botany of the foreland, and in this paper Janetschek tells the very interesting story of the animals' conquest of the place. The foreland is at an altitude of c. 7000 ft. and in less than 80 years it has changed from barren rock, stone and ice blocks into a primitive soil with a dense grass carpet. Starting from a few Collembola, spiders and beetles in the youngest zone, the fauna develops into that of a typical high alpine grassland. The study comprises worms, molluscs, millepedes, centipedes, insects, harvestmen and spiders. The mites have been collected, but so far remain unidentified. In view of the great difficulties in sampling the stony ground, problems of transport and lack of a decent laboratory, the ideal quantitative approach was not possible. In spite of this Dr Janetschek presents

a detailed picture of the qualitative and a good deal of the quantitative aspect of the fauna and the course of its establishment in these extreme localities, and the findings in the Hintereis foreland are supplemented by parallel studies in the foreland of three other glaciers. The author uses the language of certain ecological 'schools'. In some places this is a nuisance for readers not belonging to these schools. The usefulness of a technical language depends upon its universal acceptance and at least three categories of technical expressions should be excluded, viz.: (1) those for which the ordinary language has an equivalent, (2) all the 'drawers' which are too small to hold the contents allocated to them, and (3) all the words which do not convey their own meaning and even may be linguistic monsters. All of them are represented in the characteristics of *Scolioplanes acuminatus* in Table 4. The tiny animal is more or less pronounced 'euedaphisch, atmobiont, kataskaphisch-petraeisch, humicol'!

Herbert Franz (1950). *Bodenzoologie als Grundlage der Bodenpflege*. x+316 pp. Akademie-Verlag, Berlin. Price Dm. 35.

'The study of the life processes in the soil is necessary for the recognition of the interrelationships which exist in the soil between biological processes and the dead substratum...What we need for the elaboration of a biologically correct soil treatment is the exact knowledge [of all the activities] of the soil animals and the determination of the factors influencing the levels of these activities. Science must, therefore, first aim at a survey of the organisms of the soil, their numbers, activities, and requirements'. This extract from the preface gives the main idea underlying the activity of the Bundesanstalt für alpine Landwirtschaft in Admont and the book is a survey of what has been achieved so far.

Chapter 7 (228 pp.) presents the survey of the animals mentioned in the last sentence quoted, while the activities are mainly dealt with in the preceding pages. The last chapter is devoted to soil zoology as applied to agriculture.

The contents of chapter 7 are naturally and conveniently grouped. First come 32 localities from high alpine grassland at 5700–8000 ft. The presentation of the material is preceded by short descriptions of the individual localities as to vegetation and soil (general character, pore volume, organic matter content, percentage of CaO and pH). The composition of the fauna is shown in tables with an accompanying text where the author stresses the important features. The text is clear and pleasant reading and the author gives liberally of his profound knowledge of the animal life in the area. Protozoa were not studied in particular, but Varga's and Heinis's studies in similar localities are extensively quoted. Donner has studied the rotifers of several sites while nematodes were mostly done by Franz himself. Oligochaeta, molluscs and all arthropods were studied in great detail, and for some localities An Der Laan has provided information on terrestrial Turbellaria.

The next 20 sampling sites are from high alpine valleys (Schneetälchen and Schneeböden) at 5700–8000 ft. altitude. The fauna found on these 52 sites is very similar to that mentioned by Janetschek from the foreland of glaciers. In the third group of localities, comprising 67

sites in beech woods (1300–4500 ft.), the number of species increases to such an extent that the tables become almost endless. Among others they contain 110 species of beetles, 229 species of mites and 46 snails and slugs; while only 50 beetles, 102 mites and 15 snails are mentioned from the high alpine grassland. Ten sites in coniferous woods at 2000–3600 ft. reveal a very poor fauna in comparison with beech wood at the same level.

The next step takes us up into the subalpine coniferous woodland (2100–6000 ft.). The vegetation here has not been influenced by man, and the fauna is very different from that of coniferous woods at lower altitudes. The subalpine alder patches at the same altitudes are represented by 17 sites. The fauna is rich and shows several similarities to that of the low-altitude beech wood. Eighteen sites are in the sun-loving shrub vegetation at 1800–2500 ft. The fauna is very rich and comprises woodland and open land species. It is interesting to notice that the list of beetles has several species in common with an English limestone grassland. Woodland along rivers at 1900–3300 ft. harbours a fauna related to that of the previous group. The rather poor fauna of the *Erica carnea* and *Calluna vulgaris* heathland at 1800–5200 ft. was studied on 22 sites. After a consideration of the grass and herb heathland at low altitude, we are confronted with the rich fauna of grassland and fields in daily use of man, which, being derived from original woodland, is more similar to that of the various types of open land, while the pastures are richer than the land under plough. Peat moor was also studied in 19 places and the *Sphagnum* in particular in 14. The last section is devoted to a discussion of the pannonic lowland of Austria with its very different climate, soil, vegetation and fauna.

The whole chapter is a tremendous collection of biological information of the greatest interest to all terrestrial ecologists. Ecology owes much to Dr Franz and the numerous people who have assisted him in sampling, sorting and identifying probably millions of animals.

The value of the quantitative data given in chapter 7 is difficult to assess. Different sample sizes have been used for the various groups of animals. Judging from chapter 3, all sampling sites have been selected in such a way as to be typical of the area under study. A number of subsamples were taken inside 1 m.², and the pooled subsamples constitute a 'sample'. However, the reader is left in the dark as to number and size of subsamples per sample and the number of samples per site. An exact description of the procedure is badly needed in each of the 357 sites.

Chapter 5 deals with the activity of the soil animals, and the author rightly distinguishes a mechanical effect due to the movements of the animals and their way of feeding, and a chemical effect due to the digestive and excretory mechanisms of the animals. The mechanical effect of earthworms is discussed and illustrated by experiments. The chemical effect of soil animals is restricted to a discussion of their importance for humus formation. One of the most difficult problems of soil biology is tackled and, unfortunately, oversimplified. It is beyond my competence to discuss the acetyl bromide method; however, its value remains unknown, and so the results should be interpreted very carefully. The most serious criticism refers to the experiments underlying

Tables 9–11. The total absence of controls makes it impossible to draw any conclusions from the figures. Cultures consisting of several animals and leaf litter thoroughly soaked with water and kept in glass dishes for up to 3 months cannot be assumed to be bacteriologically sterile. The amount of acetyl bromide insoluble substance in the food not eaten by the animals at the end of the experiment is not given, and according to the original paper by Franz and Leitenberger (1948) it has not been determined. This invalidates the conclusions regarding animals in relation to humus formation.

The last chapter of the book on 'soil life and soil utilization' is mainly concerned with the agricultural aspects of soil zoology and falls beyond my competence.

Wilhelm Kühnelt (1950). *Bodenbiologie mit besonderer Berücksichtigung der Tierwelt.* 368 pp., 63 text-figs. and 6 plates. Verlag Herold, Strozsigasse 8, Wien, VIII. Price S 48.

This book differs from the two others in being a text-book. According to the preface the author also has in mind the student with no special zoological training. The approach to be made is the physiological and ecological one which considers 'the importance of the organisms for the formation, conservation and destruction of soils as well as the interdependence of soil organisms and plant communities (Pflanzengesellschaften)'. A short introduction (pp. 11–14) contains the pedological aspect of soil biology. The chapter on methods (pp. 15–46) is divided into three sections: techniques for observation and collection, culturing soil organisms, and preservation. This chapter is very valuable as it mentions most of the current techniques and in addition gives several practical hints from the author's personal experience. Calling to mind Gauss's wise words that the strength of a chain is the strength of its weakest link, warnings are given against assessing the number of organisms per unit area on the basis of an inadequate material.

The next chapter (pp. 47–191) is a survey of the soil animals in systematic order from Protozoa to mammals, each group under separate heading. For most groups valuable biological information is given about the number of species, geographical and topographical distribution, size and shape, nutrition, reproduction—in short, their biology. References to important biological literature and keys are given for each group.

Ten pages are devoted to the description of shapes, locomotory types, etc., in soil animals in relation to the nature of their habitat. As special features of the environment the dependence upon the composition of the soil air, water content, temperature, light, pH, and electrolytes is discussed.

The author's physiological approach to the subject reaches its clearest expression in the chapter discussing the soil organisms as an entity. The concepts of producers, consumers and reducers are introduced, and the activity of the animals is discussed in regard to their association with or direct contribution to certain decomposition processes: peat formation, dry rot, aerobic and anaerobic putrefaction, and humification. As a special case of this last process, the decomposition of leaf litter to mull and raw humus is followed. Also the decomposition of wood

is discussed in detail, especially humification but also dry, white, and red rot.

The sixth chapter deals with the various soil types and their fauna. The development and biology of Austrian rendzina and terra fusca are especially interesting. The importance of the organisms for the maintenance of soil fertility is discussed in 20 pages, and the zoogeographical aspect of the soil fauna in five. There is a valuable list of references containing more than 600 items.

An elementary text-book tends to become a compromise between the accumulation of facts and simplicity in explaining them. To the reviewer there are too many oversimplifications. There is often no clear distinction between facts and hypotheses. The borderline between soil zoology and microbiology is often approached with little success; especially, the author's concept of nitrogen fixation is curious (pp. 48, 49, 54 and 55).

A word about illustrations: to the student Figs. 5, 14, 38, 56 and 62, and perhaps others, will not convey any clear idea, because of the quality of the paper. Fig. 7 is not a good choice for an elementary text-book. Cobb's original legend to it is: 'Front view of nematode monster which feeds upon others of its kind. The drawing of the head is correct in every particular. The body has been sketched by the artist to assist the imagination in picturing how one of these organisms looks when seen from in front. The artist's conception is undoubtedly very nearly correct.'

C. OVERGAARD NIELSEN

TREE HOLE COMMUNITIES

Orlando Park, Stanley Auerbach and Glenn Corley (1940). *The tree-hole habitat with emphasis on the pselaphid beetle fauna.* Bull. Chicago Acad. Sci. 9, No. 2: 19–57. 3 text-figs. and 6 plates.

Not infrequently a fairly short monograph can tell us more, or tell it more usefully than a vast tome, because it can conveniently be read in one of those intervals of relaxation in which the ecologist explores some group of facts outside his ordinary specialization. This paper is good reading, and although the new facts are based upon only 36 tree holes investigated in the Chicago area, practically all in hardwoods, the review of knowledge about such minor habitats that precedes the special part devoted to the local survey is wide, and discusses the various kinds of tree hole that develop, their causes and the general complexity of succession and of faunal relations.

The authors point out the following features of this habitat. The bark may be opened by birds or animals, but usually it is cracked or split by storm or fire and invaded by fungal rot. In North America the fungus *Stereum gaussapatum* is an important invader. Several main kinds of succession can follow, depending on the shape and position and height of the hole and other factors, but broadly it may be underground or above ground, and if the latter, have either water or moist mould only. The ones examined were of the last type. The moisture itself varies greatly. It is considered to be rather like log mould, except for its position and the fact that decay is usually taking place in living wood, and not in dead or dying tissue. The community that develops

has much in common with the ground one among log frass, even to sound species; but is distinct in most of its species. It may be greatly complicated by such events as the invasion of the habitat by nesting birds, mammals or social insects.

The procedure was to collect the mould, and get its wet and dry weights, with extraction of the fauna by Berlese funnel in between. The only doubtful feature in the counting would seem to be the lack of any critical assessment of the efficiency of the Berlese method used, and it is not impossible that the estimates of population are lower than reality, at any rate for some groups. The material was, however, extracted for up to 15 days in some instances.

The animals were, as to numbers, mainly Collembola and mites, and of these groups mainly Entomobryidae and Oribatidae. Thus in one sample census given, out of 4600 animals in 840 g. of tree hole mould, some 93% were springtails and mites, about in equal numbers. The remaining animals were beetles, ants, spiders, pseudo-scorpions, etc. Of the beetles, carabids, staphylinids, pselaphids and ptiliids are said to be the chief families.

Twenty-six tree frogs' stomachs examined revealed a rather wide selection of foods, many of which may have been from such holes. The authors give a sensible-looking 'food web', with solid lines for ascertained food connexions, and dashed lines for suspected or expected ones.

The later section of the paper deals with the pselaphid beetles of the tree holes surveyed. This is a family of very small beetles, oddly shaped and sometimes with relatively enormous clubbed antennae. They have been shown to prefer moist darkish situations. There were about 16 individuals per hole containing any at all, with a maximum of 66, and they occurred in more than half the holes collected. Of the 12 species, one, *Euplectus confluent*, accounted for 80% of the total 343 individuals. This family of beetles is known to be predatory, and to eat such smaller animals as mites, springtails, small larvae, etc. The cover of the paper has a good drawing of one eating a mite, and the plates show, besides habitats, good line drawings of three species.

There is an excellent general literature list.

CHARLES ELTON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Several papers omitted in the last few years are being noticed in this and following issues. Papers in the *Journal of Animal Ecology* itself are not dealt with. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside, Westmorland.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1, or through a bookseller, price 3s. 6d. per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by R. Bainbridge, H. F. Barnes, A. E. Ellis, C. Elton, I. M. Goodbody, Miss U. M. Grigg, A. Macfadyen, C. Matheson, Miss E. Nelmes and Miss G. Watt; checking by B. M. Hobby; abstracting and editing by R. S. R. Fitter.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

CONTENTS

	PAGE
1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS	152
(a) Marine and brackish	152
(b) Fresh water	153
(c) Land	153
(d) Small islands	156
2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS	156
3. PARASITES	157
4. FOOD AND FOOD HABITS	158
5. POPULATION STUDIES	158
6. MIGRATION, DISPERSAL AND INTRODUCTIONS	160
7. REPORTS OF ORGANIZATIONS	161

1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(a) MARINE AND BRACKISH

Crisp, D. J. (1950). 'Breeding and distribution of *Chthamalus stellatus*.' *Nature*, Lond., 166: 311-12.

Discusses the relation of the time of breeding of this barnacle, and its density of breeding individuals, to the distribution limits as affected by temperature.

Foster, J. & Gibb, J. (1950). 'Shore feeding ecology.' *Bird Notes*, 24: 83-6.

A demonstration of the correctness of Gause's thesis that no two species with identical ecology can live side by side in the same habitat, in relation to the shore-feeding birds of a Scottish sea-loch in August. Twenty species are discussed.

Goodbody, I. M. (1950). 'Notes on Tunicata from Dublin Bay.' *Irish Nat. J.* 10: 77-80.

Mainly a list of species occurring in the area. A few notes on habitat, growth and reproduction.

Gurney, R. (1944). 'Aquatic life in the Norfolk Broads.' *New Naturalist*, 2 (6): 22-5.

A brief popular summary with some information about the fauna of these slightly brackish waters.

Jones, N. S. (1950). 'Marine bottom communities.' *Biol. Rev.* 25: 283-313.

A useful source of references and an interesting discussion of the validity on this field of the concept of the biological community. While the idea that these are bound together by biological factors is repudiated, the existence of communities, correlated with the distribution of certain physical factors, is upheld and a scheme of classification on this basis is presented. It is considered that productivity studies and detailed biological studies of the more abundant species are likely to produce more practical information than the usual type of quantitative investigation.

Williams, G. (1950). 'Distribution of *Chthalamus stellatus* on the shores of north-east Ireland.' *Nature, Lond.*, 166: 311.

This barnacle is now recorded in Antrim and Down Counties, usually above the *Balanus* zone. This is held to support the hypothesis of limitation geographically by air temperature rather than by the distribution of Atlantic water.

(b) FRESH WATER

Anon (1950). 'The published papers of D. J. Scourfield.' *Essex Nat.* 28: 195-8.

A bibliography of papers dealing mainly with fresh-water Crustacea.

Corbet, P. S. (1950). 'The dragonflies of Berkshire.' *Reading Nat.* 1: 65-7.

Contains some information on habitats.

Hickin, N. E. (1950). 'Larvae of the British Trichoptera: 28.' *Proc. R. Ent. Soc. Lond.* (A) 25: 67-70.

Tinodes waeneri (Psychomyidae) inhabits ponds, lakes and slow rivers. It is abundant in Lake Windermere where the larvae make mud tunnels on large stones or rocks 6 ft. or so from the edge of the lake. The larvae are fully described and figured.

Hickin, N. E. (1950). 'Larvae of the British Trichoptera: 29.' *Proc. R. Ent. Soc. Lond.* (A) 25: 71-4.

Lyte reducta (Psychomyidae), is a rare caddis associated with rather small, fairly rapid streams. The larva, which is fully described and figured, constructs tunnels on submerged rotting sticks. When fully grown it spins a cylindrical cocoon.

Jones, J. W. & King, G. M. (1950). 'Further experimental observations on the spawning behaviour of the Atlantic salmon (*Salmo salar* Linn.).' *Proc. Zool. Soc. Lond.* 120: 317-23.

Observations supported by cinematographic records are continued. A percentage fertilization of 97.6 was recorded for twelve nests.

Thorpe, W. H. (1950). 'Plastron respiration in aquatic insects.' *Biol. Rev.* 25: 344-90.

This is a comprehensive report on Thorpe's well-known work. The author considers the conditions under which tracheae can function under water, the usefulness of air bubbles and the functioning of the true plastron which is a gas store in the form of a very thin film. The biology of the bug *Aphelocheirus* is considered in detail. This is followed by a wider survey of plastron respiration in the Coleoptera, Trichoptera, Lepidoptera and Hymenoptera in particular.

(c) LAND

Barnes, H. F. (1950). 'The identity of the swede midge, with notes on its biology.' *Ann. Appl. Biol.* 37: 241-8.

Breeding experiments show that *Contarinia nasturtii* reared from unopened blossom of great watercress (*Rorippa amphibia*) will breed on unopened blossom of swede as well as on leaves of turnip and is in fact the same species that has been variously named *C. torquens* and *C. geisenheyneri*, pests of *Brassica* leaves and flowers. It breeds by means of unisexual families.

Basden, J. F. (1950). 'A method of distinguishing the larval stages of *Agriotes sputator* (L.) (Col., Elaterid.)' Bull. Ent. Res. 41: 395-413.

Measurements of total length or of various parts are not any good, but the number of teeth on the mesothoracic and abdominal spiracles increases with age. The average numbers of teeth on the two thoracic or on all the abdominal spiracles fell into eight groups which represent growth stages and not necessarily instars. 80% of the larvae can be placed in their correct growth stages by counting the teeth on one spiracle only; for less than 1% it is necessary to examine as many as five spiracles. An accuracy of 97% can be maintained.

Brown, P. E. (1948). 'Woodland tits.' New Naturalist, 1: 52-5.

A popular account of the Paridae found in British woodlands, indicating how they are separated ecologically.

Brown, E. S. & Duncan, A. B. (1949). 'A list of the Tipulinae (Diptera Nematocera) of the Solway area, with some notes on the habitats of the adults.' Scot. Nat. 61: 156-68.

Currie, P. W. E. (1950). 'Some notes on the birds of the bombed sites.' Lond. Nat. 29: 81-4.

Observations on the habits of eight breeding species and particulars of 23 casual visitors.

de Worms, C. G. M. (1950). 'The butterflies of London and its surroundings.' Lond. Nat. 29: 46-80.

Notes on the habitats, distribution, abundance and seasonal appearance of the 56 species now represented in the London area and two that are extinct, with a short review of the main habitats in the area and a discussion of the more striking changes that have occurred in the frequency of the species during the past 50 years. Very few resident species have been lost, and many local ones appear to be steadily spreading.

Downes, J. A. (1950). 'Habits and life-cycle of *Culicoides nubeculosus* Mg.' Nature, Lond., 166: 510-11.

This midge was studied in Dorset, where its larvae live in dung-contaminated water of hoof-prints of cattle in farm-yards, and the adults not far away. The adults need a blood meal before oviposition, but do not bite man except in the laboratory, and may depend on horses. The paper describes swarming habits of the males, mating behaviour, diet activity of the females (at dusk and dawn mainly), egg-laying, biting habits and longevity of the female in the laboratory (about 1 month).

Edwards, E. E. & Evans, J. R. (1950). 'Observations on the biology of *Corymbites cupreus* F. (Coleoptera, Elateridae).' Ann. Appl. Biol. 37: 249-59.

Field life history—beetles on the wing in May and June, egg-laying in June, egg stage about 34 days, larval stage probably 5 years, pupation towards end of July or beginning of August. Beetles emerge after about 21 days and do not always remain overwinter in the earthen pupal cells. Food of larvae chiefly roots and underground stems, also decayed organic matter in the soil. Enemies include crows and the carabid beetles *Pterostichus madidus*, *Nebria brevicollis* and *Harpalus ruficornis*. Parasites include a Hymenopteron and the fungi *Metarrhizium anisopliae* and *Syngliocladium cleoni*.

[**Ellis, G.**] [1950]. 'Butterflies and moths of the local area.' Proc. Llandudno, Colwyn Bay and District Field Club, 22 (1949): 21-5.

A list of 41 butterflies taken within 25 miles of Llandudno. *Nymphalis polychloros* was observed at Llandudno over 50 years ago and after a period of great scarcity or extinction reappeared in 1944. *Hamearis lucina* (a single specimen in 1943) and *Cupido minimus* (two in 1944). *Lycaena phloea*s and *Callophrys rubi* are scarce near the coast, but common elsewhere. *Celastrina argiolus* was formerly rare, but has become much more plentiful since 1940.

Escritt, J. R. & Arthur, J. H. (1948). 'Earthworm control.' J. Bd Greenkeeping Res. 7: 162-72.

A summary of modern methods of controlling earthworms on sports turf.

Fisher, J. (1950). 'The black rat, *Rattus rattus* (L.) in London.' Lond. Nat. 29: 136.

This rat occurs in many places up to 3 miles from the river and is established in some at still greater distances. It is dominant in the Oxford Street area and is the only rat in some buildings that are proofed at ground level. Areas and boroughs where control measures are regularly employed and boroughs in London and towns near it where black rats have recently been recorded are listed. All colour forms occur and interbreed, and are not considered to be of subspecific rank.

Ford, E. B. (1948). 'Woodland butterflies.' *New Naturalist*, 1: 47-50.

A popular account of the distribution of the woodland butterflies of the British Isles, with maps.

Goodey, T. (1950). 'Stem eelworm and clover.' *Proc. Ass. Appl. Biol. in Ann. Appl. Biol.* 37: 324-7.

Susceptibility of various clovers and legumes, biological race differences, true symptoms set up by red clover eelworm, dispersal of the parasite as a seed-borne organism.

Johnson, C. G. (1950). 'Infestation of a bean field by *Aphis fabae* Scop. in relation to wind direction.' *Ann. Appl. Biol.* 37: 441-50.

Wind direction gave a plausible explanation of the infestation pattern round the edge of a bean field; but other factors are involved.

Jones, F. G. W. (1950). 'Observations on the beet eelworm and other cyst-forming species of *Heterodera*.' *Ann. Appl. Biol.* 37: 407-40.

Beet eelworm attacked Polygonaceae, Chenopodiaceae, Amarantaceae, Aizoaceae, Caryophyllaceae, Cruciferae, Onagraceae, and Labiatae. *Galeopsis* eelworm attacked several families including Chenopodiaceae, Caryophyllaceae and Labiatae. Other root eelworms were more specific; the carrot-eelworm attacked only cultivated and wild carrots; the potato eelworm only the genera *Solanum* and *Lycopersicum*; the pea eelworm attacked only peas, beans and tares. The maximum number of generations for the beet, potato, pea and carrot eelworms is between two and three a year, but is governed by the vegetative period of the host crop. *Heterodera carotae* is described and the status of the *Galeopsis*-root eelworm is discussed.

Jones, J. Morgan (1950). 'Clover seed weevils.' *Proc. Ass. Appl. Biol. in Ann. Appl. Biol.* 37: 313-20.

Life history and biology, particularly of *Apion aestivum*.

Miles, M. (1950). 'Observations on the biology and control of cabbage root fly, *Erioischia brassicae* (Bché).' *Ann. Appl. Biol.* 37: 260-7.

Egg-laying began in third week of April, reached its maximum in the fourth week and first week of May and continued until early April. Eggs on soil were almost exclusively those of *Erioischia brassicae*; those on plants mainly *Pegohylemyia fugax* with some *Erioischia brassicae* and *Delia cilicrura*. Larvae present from fourth week of April to mid-January. A washing technique for separating larvae from the soil and plant is described. Puparia vary greatly in size; the small ones were heavily parasitized by cynipid wasps.

Miles, M. (1950). 'Studies of British Anthomyiid flies.' *Bull. Ent. Res.* 41: 343-54.

Eggs of *Chortophila cilicrura* were found in soil crevices and on vegetation in contact with soil; it is suggested that the larvae are primary scavengers on organic matter in the soil. Larval feeding period in May to June 8-16 days, 15-24 days in October to November. Pupal stage 16-21 days in May to June, 5 weeks to 5 months in autumn and winter. The flies, which live up to 79 days, are attracted to moist freshly turned soil from April to October. Parasitism by the nematode *Heterotylenchus aberrans* occurred. The eggs of *Pegohylemyia fugax* were found on various parts of several brassicas. The larvae were reared in decomposing vegetation. Pupation takes place in the soil and in the feeding sites. Life cycle 4-5 weeks in spring; winter passed as puparia.

Morley, A. (1941). 'The behaviour of a group of resident British starlings (*Sturnus v. vulgaris* Linn.) from October to March.' *Naturalist*: 55-61.

Regular observations were carried out on a group of Oxford starlings; there was a marked difference in behaviour between these resident birds and the birds in large flocks on nearby pasture land which were probably of Continental origin.

Niblett, M. (1950). 'Plant galls of Bookham Common.' *Lond. Nat.* 29: 90-2.

From 3650 smooth galls of *Rhodites* sp. collected chiefly from *Rosa canina* during 1941-44 there emerged 85 *Rhodites dispar*, 83 *R. eglanteriae*, parasites comprising 1891 Chalcids of five species and 57 Ichneumonids (*Orthopelmar brevicornis*), and 792 inquilines (*Periclistus caninae*).

Robinson, W. (1950). Montagu's harriers (*Circus pygargus*). *Bird Notes*, 24: 103-14.

Mainly concerned with the breeding biology of *C. pygargus*, but some details on food and nest site.

Tomlin, J. R. le B. (1949-50). 'Herefordshire Coleoptera.' [Id.] 'Part I' (pp. 1-30, 1949): 'Part II' (pp. 31-64, 1950). Woolhope Nat. F. C., Broad Street, Hereford. Price 2s. 0d. each.

A faunistic list, with some details of habitat.

Wilson, G. F. (1950). 'Pests of flowers and shrubs.' Bull. Minist. Agric. Fish. No. 97: 105 pp. H.M. Stationery Office, London. Price 4s. 6d.

A very well-illustrated and authoritative brochure on garden pests (including not only insects, but molluscs, woodlice and millipedes), with instructions for control measures.

(d) SMALL ISLANDS

Fisher, J. (1948). 'St Kilda, a natural experiment.' New Naturalist, 1: 91-108.

Contains a good deal about the animal and bird populations, and in particular about the biotic effect of man upon them.

Fisher, J. & Piercy, K. (1950). 'Notes on Eilean Bulgach, Sutherland.' Scot. Nat. 62: 26-30.

Estimates of breeding populations of the birds of the island.

Gillham, M. [1950]. 'Some of the chief effects of the birds and mammals in the modification of the vegetation of Skokholm Island.' Skokholm Bird Observatory Rep. for 1949, 31-4.

Burrowing by rabbits, shearwaters and puffins, treading by various sea-birds, and grazing by rabbits are the principal biotic factors affecting the vegetation.

Harrison, J. W. Heslop (1948). 'The passing of the Ice Age and its effect upon the plant and animal life of the Scottish Western Isles.' New Naturalist, 1: 83-90.

A popular presentation of the case for the survival of certain species in the Outer Hebrides on nunataks and cliff ledges.

Jones, M. H. [1950]. 'A preliminary report of habitat distribution of the harvestmen (Opiliones) of Skokholm.' Skokholm Bird Observatory Rep. for 1949, 38-40.

Only four species occur on this Pembrokeshire island.

[**Lacey, W. S.] [1950].** 'Ecological Studies on Puffin Island.' Proc. Llandudno, Colwyn Bay and District Fld Cl. 22 (1949): 26-34.

A general account of the geology, history and natural history, with lists of the birds and plants and their distribution on the island and notes on the effects of man, grazing animals and sea-birds on the soil.

Vevers, H. G. (1948). 'The natural history of Ailsa Craig.' New Naturalist, 1: 115-21.

A brief popular account which includes some discussion on the ecology of the birds of this large rock off the coast of Ayrshire.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Johnson, C. G. (1950). 'The comparison of suction trap, sticky trap and tow-net for the quantitative sampling of small air-borne insects.' Ann. Appl. Biol. 37: 268-85.

The sticky trap and stationary aerial tow-net catch insects which alight or fly on to them or are blown against them by the wind. They are inefficient in light winds and in calm weather. The suction trap samples a constant quantity of air in all relevant wind-speeds and in perfectly calm weather.

Kennedy, J. S. & Booth, C. O. (1950). 'Methods for mass rearing and investigating the host relations of *Aphis fabae* Scop.' Ann. Appl. Biol. 37: 451-70.

A 'production-line' arrangement of eleven ventilated breeding cages, with additional cages for starting subcultures and rearing alatae, all contained in a portion of a small glasshouse with supplementary lighting in winter. An 'aphid-gun', a modified type of aspirator catcher, is described for handling and counting aphids. A modified technique involving two types of small metal cages for host-transference experiments is described. By this means individual leaves can be compared as host-units.

Sankey, J. H. F. (1950). 'British harvest-spiders.' *Essex Nat.* 28: 181-91.

A useful summary for beginners in the group, dealing with taxonomy, identification, bionomics, ecology, migration, distribution in the British Isles, collecting and preservation.

Stroyan, H. L. G. (1950). 'Recent additions to the British Aphid fauna. Part 1: *Dactynotus* Rafinesque to *Rhopalosiphum* Koch, C.L.' *Trans. R. Ent. Soc. Lond.* 101: 89-123.

Thirty-four species since G. S. Kloet and W. D. Hincks (1945, *A check list of British insects*, Stockport).

Stroyan, H. L. G. (1950). '*Jacksonia papillata* Theobald (Hemiptera, Aphididae): a redescription with biological and taxonomic notes.' *Proc. R. Ent. Soc. Lond. (B)* 19: 90-5.

The apterae feed very low down on the colourless basal portions of the stems of *Poa pratensis*.

3. PARASITES

Allan, R. M. (1950). 'Fleas (Siphonaptera) from birds in north-east Scotland.' *Scot. Nat.* 62: 33-41.

Nine out of the 13 known Scottish species were found during 1949, and in addition a species new to Britain, *Frontopsylla laetus* Jordan.

Cameron, E. (1950). 'The biology and economic importance of *Alomya debellator* (F.), a remarkable parasite of the swift moth, *Hepialus lupulinus* (L.).' *Bull. Ent. Res.* 41: 429-38.

Life history, including arrested development in the first instar larva. Diagnostic characters for primary and mature larval stages. *Alomya debellator* is in some areas the most important single factor of biological control of the underground-living larvae of *Hepialus lupulinus*.

Hick, A. E. (1949). 'Dock weevils and their enemies.' *Country-side*, 15: 36-8.

A popular account of the life history and parasites of *Phytonomus (Hypera) rumicis*.

Dunnet, G. M. (1950). 'Fleas (Siphonaptera) from mammals in Aberdeenshire.' *Scot. Nat.* 62: 42-9.

An examination of fleas recorded from about 500 small mammals during 1948-49 to determine the frequency of different species of fleas on different host species in the region.

Jones, B. M. (1950). 'Experimental rearing of the British harvest mite to the adult stage.' *Nature, Lond.*, 166: 823.

Hitherto it has been difficult or impossible to rear *Trombicula autumnalis* beyond the nymphal stage. Details of feeding and maintenance of each stage are given.

Savage, R. M. (1950). 'Observations on some natural epizootics of the trematode *Polystoma integerrimum* among tadpoles of *Rana temporaria temporaria*.' *Proc. Zool. Soc. Lond.* 120: 15-37.

A quantitative study of the incidence of parasitism with a description of the parasite and its biology. It appears not to have any harmful effect on the tadpoles, and infection, which is very irregular in its incidence, is confined to the later stages of larval life. The rates of reproduction of the two species and the intensity of infection are considered.

Smith, K. M. (1950). 'Virus diseases of insects.' *Discovery*, 11: 175-78.

A popular summary of the subject.

4. FOOD AND FOOD HABITS

Fox, H. M., Gilchrist, B. M. & Phear, F. A. (1950). 'Functions of haemoglobin in *Daphnia*.' *Nature*, Lond., 166: 609-10.

Blood haemoglobin is synthesized by *Daphnia* (species not mentioned) in response to oxygen shortage. This prevents asphyxia, and increases the speed of feeding and the number of eggs. *Daphnia* living in waters poor in oxygen are pinker than those in well-aerated waters.

Roberts, E. N. (1950). 'Artificial feeding of *Culicoides nubeculosus* in the laboratory.' *Nature*, Lond., 166: 700.

This species bites horses and cattle in nature, but can be maintained by biting man in the laboratory. A simpler method is described, in which the midges suck stocked ox blood through a membrane of chicken skin. By using heparinated ox blood about two-thirds oviposition of the female midges was obtained, equal to those fed directly on man.

Roebuck, A. (1949). 'Notes on the economic zoology of Lincolnshire during 1948.' *Trans. Lincs. Nat. Union*, 12: 116-18.

Mainly insect pests, with their foods.

Stubbs, E. (1950). 'Winter food of robin.' *Naturalist*: 102.

Analysis of four pellets provided evidence of the food which robins obtain naturally in winter.

5. POPULATION STUDIES

Anon. (1950). 'A survey of local rookeries: ten years' progress.' *Hastings and E. Sussex Nat.* 7: 175-82.

The number in use increased from 55 to 93 during 1939-49, nine sites having been abandoned.

Ashton, K. B. (1948). 'The problem of the corn-crake.' *New Naturalist*, 1: 161-4.

A popular account of the decrease of *Crex crex* over most of the British Isles, and of its possible explanations.

Blathwayt, F. L. (1949). 'The chequered skipper (*Carterocephalus paluemon*) in Lincolnshire.' *Trans. Lincs. Nat. Union*, 12: 91-3.

Discusses possible reasons for its decline.

Campbell, B. (1950). 'Breeding of stock-doves at Hordley, nr. Woodstock, 1949.' *Rep. Oxf. Orn. Soc. for 1949*: 42.

Brief details of egg and young production in a colony containing 18 nest-sites.

Clementson, G. (1949). 'The long-tailed duck in Manx waters.' *Peregrine*, 1: 22-3.

Clangula hyemalis was not recorded in Manx waters till 1928, since when it has been seen in every year but three (excluding the war years). The fact that it has no old Manx name, though vernacular names exist elsewhere in the British Isles, suggests that this may be a genuine extension of range.

Colquhoun, M. K. (1949). 'Woodland bird communities.' *New Naturalist*, 1: 57-65.

A popular account of the bird populations of British woodlands.

Cramp, S. (1950). 'The census of swifts, swallows and house-martins, 1949.' *Lond. Bird Rep.* 14: 49-57.

In a breeding census taken in four sample areas, totalling about 24½ sq. miles and situated in Inner London, the inner and outer suburbs, and on the outskirts, the numbers of nests found were 163, with a further probable 58, for swifts, 53 for house-martins, and 4, probably 5, for swallows. No nests occurred in Inner London. Swifts and house-martins were most numerous in the inner suburbs and decreased gradually towards the outskirts, where almost all the swallows were found. The most important factors influencing distribution are believed to be availability of food supplies and suitable nesting sites. 96.2% of the swift's nests were within half a mile of water, and house-martins were also most numerous near water, which provides a plentiful food supply and, for the former, mud for nests. Swallows' nests were confined to farm buildings.

Cramp, S. (1950). 'Chick survival in the kittiwake.' *Scot. Nat.* 62: 63-4.

A count of 220 nests on the Isle of May (Fife), compared with a previous count in 1936.

Cramp, S. & Teagle, W. G. (1950). 'A repeat bird census of Kensington Gardens.' *Lond. Bird Rep.* 14: 41-8.

About the same number of species was recorded in three counts during the winter of 1948-9 as in four in that of 1925-6, but the number of individuals was reduced by about half, largely owing to a decrease of about one-third in house-sparrows. Six species showed a marked increase, attributed in the case of blackbirds, tufted duck, black-headed gulls and common gulls to a general increase over the country, and in that of the jay to adaptation to urban conditions. Six species showed a marked decrease. Moorhens and, possibly, house-sparrows may be experiencing a general decline; the decrease of wrens is probably caused by removal of cover and increased interference, that of wood-pigeons is attributed to persecution, and that of mallard in part to increases in gulls. The great reduction in starlings is unexplained. The most highly populated habitats were shrubberies and flower-beds (609 birds per 10 acres), water (458), lawns adjoining water (398) and lawns (293), and the lowest were woodland open to the public and without undergrowth (5) and open grassland with scattered trees (28). Over 80% of 2528 house-sparrows (the most abundant bird) occurred in the shrubberies and flower-beds, which occupied only 13 acres of a total of 274. The highest numbers of species were found in woodland and open grassland (18 and 14, respectively) and the lowest in shrubberies and flower-beds, allotments, and lawns (12, 7 and 7, respectively).

Fitzgerald, B. Vesey- (1941). 'The noctule.' *Naturalist*: 157-61, 189-98, 233-9.

Includes many interesting observations on this species and deals particularly with 4 years' population studies of a male and female colony.

Fisher, J. (1949). 'The death of birds.' *New Naturalist*, 2 (5): 36-8.

A popular summary of what is known of the longevity and causes of mortality of British birds.

Kettle, D. S. (1950). 'The seasonal distribution of *Culicoides impunctatus* Goetghebuer (Diptera: Heleidae (Ceratopogonidae)) with a discussion on the possibility that it may be composed of two or more biological races.' *Trans. R. Ent. Soc. Lond.* 101: 125-45.

Seasonal distribution at Loch Lomond in 1947, 1948 and 1949 was bimodal. There were sufficient larvae present in the soil at the end of May to account for a full second period of emergence, the sex ratio of the two populations was significantly different and the vertical and horizontal distributions were also different. Therefore the hypothesis of two biological races at Loch Lomond is put forward. There may be a third at Liverpool.

Parrinder, E. R. (1950). 'The census of great crested grebes 1949.' *Lond. Bird. Rep.* 14: 38.

Numbers of *Podiceps cristatus* in the London Area in 1949 showed an increase of 7% over the previous year; in Surrey numbers increased 65%. During 1946-8, there were more birds on lakes and reservoirs than on gravel-pits, but by 1949 many gravel-pits, especially in south-western Middlesex, had been filled in and the reverse was true. Complete breeding records were not made, but the number of pairs with nests of young had increased from 57 in 1948 to 87.

Rainier, I. (1950). 'Some rough notes on the altered status of birds in North Fambridge, Essex.' *Essex Nat.* 28: 198-200.

Compares the periods 1935-9 and 1945-9 on the Crouch estuary.

Sang, J. H. (1959). 'Population growth in *Drosophila* cultures.' *Biol. Rev.* 25: 188-219.

In this paper the logistic law of population growth is criticized and it is maintained that the adherence to the law, despite obvious inconsistencies with the conditions found in nature, has inhibited further work. These conclusions are based on some experiments with *Drosophila* cultures in which many complicating factors are present due to the discontinuous development of the fly, and numerous interactions between yeasts, adults and larvae and the environment. The implications of such a situation for genetical studies on small populations are stressed.

Spittle, R. J. (1950). 'The rook population of the middle Thames valley (No. 2).' *Middle-Thames Nat.* 2: 34-5.

The number of nests in the whole area increased from 742 to 986 between 1947 and 1949, but in the immediate neighbourhood of the town of Slough an increase of only two nests was recorded in this period, and since 1932 a decrease from 112 to 41 nests.

- Stratton, L. W. (1950).** 'The land Mollusca of the parish of Aldenham: a re-survey.' Trans. Herts. Nat. Hist. Soc. 23: 100-27.

A repeated survey of this parish revealed all but two of the species found in the earlier survey by A. E. Boycott of 1915-18, plus seven additional ones, in spite of a considerable increase in the built-up area. Some species had increased and extended their range. Distribution is related to both subsoil and habitat, and the influence of microclimate is illustrated.

- Wadley, N. J. P. (1950).** 'Black redstarts in the London Area 1949.' Lond. Bird Rep. 14: 39-41.

Breeding records for the 11 pairs (the maximum yet recorded) of *Phoenicurus ochrurus* that bred in the City are summarized and non-breeding records for Inner and Outer London, Surrey, Middlesex and Kent are listed. Most pairs were two-brooded, but one raised three broods and four one each, and there were at least 76 fledglings. Usual fledging dates for the first and second broods were 19 May-4 June and 3-28 July, respectively. Two new breeding areas were found in Inner London.

- Ward, B. T. (1950).** 'Notes on a swarm of dipterous flies.' Essex Nat. 28: 212-13.

A large swarm of *Sepsis fulgens (tonsa)* of both sexes on *Molinia caerulea* in Epping Forest in September, with references to a few other swarms of the same and congeneric species.

- Watson, J. S. (1950).** 'Some observations on the reproduction of *Rattus rattus* L.' Proc. Zool. Soc. Lond. 120: 1-12.

Observations on 2612 rats from buildings in the Port of London, 1519 from the docks and 1358 from Cyprus form the material for this paper. Sexual maturity in the female is reached at a higher body weight between November and March than during the remaining months. Pregnancy rate is highest on the ship rats and number of embryos is correlated with the weight of the females. At least 25% of embryos are lost between implantation and full term. The proportions of the three colour forms in ships is the same as that among the shore populations.

- Wickens, J. C. (1949).** 'Rook and jackdaw roosts in the Rye district.' Hastings & E. Sussex Nat. 7: 129-36.

Observations for 3 consecutive years.

- Worthington, E. B. (1950).** 'An experiment with populations of fish in Windermere, 1939-48.' Proc. Zool. Soc. Lond. 120: 113-49.

The paper surveys the effects of extensive trapping of over four million perch throughout this period and of netting pike after 1944; both the bionomics of these species and also of the char, trout and minnows present are considered. Evidence is presented to show that the char and minnows have increased in size and in numbers. One unexpected result is that there has, as yet, been no change in the growth rate of the perch despite greatly reduced competition. That larger fish have been caught by anglers is attributed to the males being more frequently trapped than the females and the younger fish more than the older. The biology and migrations of the perch have been studied in detail.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

- Barnes, H. (1950).** '*Sagitta setosa* J. Müller in the Clyde.' Nature, Lond., 166: 447.

The presence of this chaetognathan indicates that in autumn there is some movement of Irish Sea water into the Clyde area, *Sagitta setosa* being a regular Irish Sea species, but hitherto unknown in the Clyde, where *S. elegans* occurs.

- Fitter, R. S. R. (1950).** 'Man's additions to the British fauna.' Discovery, 11: 58-62.

A summary of the species of terrestrial vertebrates introduced into the British Isles by human agency.

- Glegg, W. E. (1950).** 'Introduction of wels or catfish into Hertfordshire.' Trans. Herts. Nat. Hist. Soc. 23: 131.

Silurus glanis was introduced to Tring Reservoirs about 1906 and appears to have become established.

- Hebditch, G. A. (1950).** 'Waxwings in Britain.' Country-side, 15: 236-8.

A summary of occurrences of *Bombycilla garrulus* in the British Isles during the irruption of the 1949-50 winter, with a few notes on food.

Hooper, W. M., Hooper, J. H. D. & Shaw, T. R. (1950). 'Some observations on the distribution and movements of cave-dwelling bats in Devonshire.' *Naturalist*: 149-57.

During recent years some 740 bats (mainly *Rhinolophus ferrum-equinum* and *R. hipposideros*) have been banded, and a recovery rate of 58 % has been reached for the first-named species. As a result information has been obtained about the length of flights, sleeping habits and proportion of the sexes.

Matthews, G. V. T. (1949). 'Bird navigation.' *New Naturalist*, 1: 146-55.

A popular account of what is known of how birds orientate themselves, both on migration and under experimental conditions.

Palmer, R. (1950). 'The midwife toad in Bedfordshire.' *Country-side*, 15: 225-6.

A small colony of *Alytes obstetricans* became established in a nurseryman's garden in Bedfordshire about 1878 (whether deliberately or accidentally is not known). About 1920 the original locality was built over, but a number of toads were transferred to two other gardens in the town, where they still survive and breed.

Pennie, I. D. (1950). 'The Tongue badgers.' *Scot. Nat.* 62: 54-5.

Meles meles is re-introduced in the Tongue district of north Sutherland.

Rieser, D. E. (1950). 'Fish migration.' *Discovery*, 11: 184-5, 201.

A popular summary of migration in the herring, mackerel, salmon and eel.

Scott, P. (1948). 'The migration of wild geese.' *New Naturalist*, 1: 156-60.

A popular account of the migrations of the geese that visit the British Isles.

Shorten, M. (1948). 'Grey squirrels in Britain.' *New Naturalist*, 1: 42-6.

A brief account of the habits, biology and spread of this introduced species, with maps showing the range of both *Sciurus carolinensis* and the native *S. vulgaris* in 1944-5.

Stubbins, H. G. (1950). 'Earlier records of *Elminius modestus* Darwin in British waters.' *Nature*, Lond., 166: 277-8.

This Australasian barnacle had been known here since 1945. This note records some earlier records back to 1943, in the English Channel.

7. REPORTS OF ORGANIZATIONS

Carlisle Natural History Society (1949). Report for the session 1948-9. 16 pp.

In addition to details of the Club's activities during the year, contains a short list of unusual birds seen in the district, and other notes, including a statement that the blue hare (*Lepus timidus*) has become established in the Bewcastle and Gilsland moors.

des Forges, G. & Harber, D. D. [1950]. The Sussex Bird Report, 1949. 28 pp. (G. des Forges, The Vale, Ovingdean, Brighton, Sussex, 5s.)

Notes on migration in addition to the usual faunistic notes.

Devon Bird-watching and Preservation Society [1950]. Twenty-second Report, 1949. 81 pp.

A faunistic list of the birds of Devon during the year, with special reports on the migration of the wheatear, swallow, house-martin, swift and black redstart.

Fair Isle Bird Observatory (1950). First Annual Report, 1949. 32 pp. (17 India St., Edinburgh 3, 2s. 6d.)

Mainly concerned with bird migration at this famous observation point, but with notes also on the breeding birds and bird parasites.

International Committee for Bird Preservation: British Section (1950). Annual Report for 1949. 40 pp. (c/o British Museum (Nat. Hist.), London, S.W.7, 2s.)

Includes reports on the work of the International Wildfowl Institute, the wildfowl counts promoted by the Wildfowl Inquiry Committee, and the ringing of wild duck at ringing stations and decoys at Abberton (Essex), Abbotsbury (Dorset), Borrough Fen (Northants) and Orielton (Pembrokeshire).

The King's School, Canterbury, Natural History Society and Field Club (1947). Annual Report, 1946-7. 40 pp. (Price 2s. 6d.)

Contains a survey of the fauna of the Stodmarsh area, where subsidence due to mining operations has created a large marsh in the Stour valley east of Canterbury (mainly mammals, birds, reptiles and Amphibia, but some fresh-water invertebrates), also some notes on the effect of the severe winter of 1946-7 on the wild life, mainly birds, of the district.

Liverpool Naturalist's Field Club (1949). Proceedings and Natural History Notes for the Area, 1948. 26 pp. (Price 1s. 6d.)

Contains faunistic notes on the Rotifera, Cladocera, humble-bees and birds, and a short paper on changes in status and distribution of some Wirral birds since 1874.

London Natural History Society (1950). 'City bombed sites survey.' Lond. Nat. 29: 81-4.

Includes notes on birds by P. W. E. Currie comprising observations on the habits of eight that breed or are presumed to breed there and a list, with numbers, dates and other particulars, of 23 casual visitors.

London Natural History Society (1950). 'The survey of Bookham Common. Eighth Year.' Lond. Nat. 29: 89-133.

An introductory progress report of work in 1949 includes notes by C. J. F. Bensley on the recolonization by fresh-water molluscs of two ponds that were drained in the previous year and on the trends observed in other ponds and streams, and a statement by G. Beven that the number of complete territories held by wrens and robins in a wood of about 40 acres was 16 and 22, respectively. M. Niblett lists the plant-galls recorded since 1945 [see also section 3]. P. W. E. Currie compares the 1949 breeding populations (estimated as singing males) of a resident and a summer immigrant bird for each of four habitats in an area of grassland that was fired in March 1948 with those in that year, and concludes that only the two (yellow bunting and tree-pipit) from the open grass itself showed a marked decrease. L. Parmenter gives an annotated systematic list showing the distribution, seasonal appearance of adults, habits and habitats of over 700 Diptera (including two new to the British Isles) collected in the area during 1935-50 and other lists of adults collected at fungi, carrion, dung, and flowers of different colours; colour appears to be of little importance in attracting flies, but those that fly close to the ground visit only short-stemmed flowers.

Lundy Field Society (1950). Third Annual Report, 1949. 52 pp. (L. A. Harvey, University College, Exeter, 2s. 6d.)

In addition to the usual faunistic notes on the birds seen during the year, there are accounts of bird migration, censuses of nesting sea-birds, the growth of nestling shags (*Phalacrocorax aristotelis*), and a list of myriapods found on the island.

Royal Society for the Protection of Birds (1950). Bird-Protection, 1949: 58th Annual Report. 52 pp. (R.S.P.B., 82 Victoria St., London, S.W.1, 2s.)

Mainly concerned with the technical and educational problems of bird protection, but there is an article (reprinted from *The Times* of 10 January 1950) summarizing the history of the avocet (*Recurvirostra avozetta*) population of the British Isles during the present century, and some faunistic notes on the birds of the sanctuaries at Minsmere Level and Havergate Island in Suffolk.

Severn Wildfowl Trust (1949). Second Annual Report, 1948-9. pp. 64. (Country Life, 7s. 6d.)

Includes details of the wild goose population at New Grounds (Gloucestershire), the operation of the decoy, faunistic notes on other wild birds, and a note on some homing experiments with moorhens.

Skokholm Bird Observatory [1950]. Report for 1949. 40 pp. (West Wales Field Society, The Red House, Tenby, Pembrokeshire, 2s. 6d.)

In addition to faunistic notes on the mammals, birds, reptiles, Amphibia and Lepidoptera of the Pembrokeshire islands of Skokholm and Grassholm, there is a short paper on the razorbill (*Alca torda*) population, a note on the habitats of ants, and papers on the effects of birds and mammals in modifying the vegetation, on the intestinal Basidiomycetes of a domestic horse, and on the habitat distribution of the Opiliones.

Slough Natural History Society (1949). The Middle-Thames Naturalist. 32 pp. (Price 2s. 6d.).

The first issue of this journal contains the reports of the Society for 1947-8, with lists of the mammals and birds seen during the period (a colony of feral coypus is in the area), a short note on the rook population of the middle Thames valley, and some notes on wasps of the genera *Vespa* and *Vespula* around Slough, Buckinghamshire.

Smith, A. E., Smith, M. & Ottaway, C. L. (1950). Bird Observatory and Field Study Centre, Gibraltar Point, Lincolnshire. Report for 1949. 38 pp.

Report on the first year's work of the observatory, mainly on bird migration, with some notes on breeding birds and on butterflies.

Staton, J. [1950]. Report on the birds of Nottinghamshire for the years 1946 to 1949 inclusive. 56 pp. (Trent Valley Bird Watchers, 41 Besecar Avenue, Gedling, Notts, 6s.)

Faunistic notes, and a short paper on the migration of swifts at Thurgarton in the autumn of 1949.

Ticehurst, N. F. (1950). Notes on the local fauna and flora for 1949. Hastings & E. Sussex Nat. 7: 183-208.

Mainly birds and butterflies, but includes details of the spread of the introduced frog *Rana ridibunda* into E. Sussex.

Uppingham School Field Club (1949). Report for 1948-9. 70 pp.

Contains faunistic notes on birds, butterflies, moths, mammals, reptiles and amphibians, some notes on the migration of the swift (*Apus apus*), on the fauna of a pond with a diagram, and on the habits of the badger (*Meles meles*).

Williamson, K. (1949). Fair Isle Bird Observatory: First Report, 1948: Part II—Migration. Scot. Nat. 61: 129-43.

Species notes on migratory birds in the autumn of 1948.

